Systematic Zoology

SOCIETY OF SYSTEMATIC ZOOLOGY

UNIVERSITY OF MICHIGAN
NOV 11 1953
Museum Library
MUSEUMS LIBRARY

An Improved Graphical Analysis	*C. L. Hubbs and C. Hubbs*	49
Regularity of Form in Organisms	*M. M. Novikoff*	57
The Systematics of Vertebrate Larvae	*G. L. Orton*	63
Factor Analysis in Termite Systematics	*C. P. Stroud*	76
Mayr, Linsley, Usinger: "Methods . . ."	*C. L. Hubbs*	93
People and Projects		95

VOLUME 2 JUNE 1953 NUMBER 2

Systematic Zoology

JOHN L. BROOKS, *Editor*

Editorial Board

P. J. DARLINGTON, JR. G. E. PICKFORD
L. R. DICE C. W. SABROSKY
G. W. SINCLAIR

SYSTEMATIC ZOOLOGY is published quarterly, on or about the tenth day of March, June, September, and December, by the Society of Systematic Zoology. Manuscripts and correspondence about the contents of the journal and other editorial matters should be addressed to the editor, Dr. John L. Brooks, Osborn Zoological Laboratory, Yale University, New Haven, Conn.

Subscription rates are $4.00 to members, $7.00 to non-members and institutions. The price of single numbers, when available, is $1.50 to members and $2.00 to non-members. Annual dues are $1.00. Correspondence regarding subscriptions, membership, purchases, non-receipt, and other non-editorial business should be addressed to the secretary-treasurer of the Society, Dr. R. E. Blackwelder, Room 429, U. S. National Museum, Washington 25, D. C.

The Society of Systematic Zoology

OFFICERS FOR 1953

President.....H. B. HUNGERFORD
University of Kansas

President-Elect.....H. W. STUNKARD
New York University

Secretary-Treasurer.....R. E. BLACKWELDER
U. S. National Museum

THE COUNCIL

G. F. FERRIS	1953	K. P. SCHMIDT
C. C. HOFF	1954	G. W. WHARTON
D. F. HOFFMEISTER	1955	H. W. MANTER
J. S. ROGERS	1956	H. M. SMITH

Entered as second-class matter at the post office at Washington, D. C., with an additional entry at Baltimore, Maryland.

An Improved Graphical Analysis and Comparison of Series of Samples

CARL L. HUBBS and CLARK HUBBS

OVER the past few decades graphical methods have been developed and increasingly used for the comprehensive analysis and for the rapid and economical comparison of series of samples. These methods are applicable to any type of data involving random variation, but are of particular concern to systematists, who are constantly confronted with data derived from series of varying samples.

In his pioneering study of variation and speciation in the garter snakes (*Thamnophis*), Ruthven (1908) showed by graphs the range, the mean, and the number of specimens for the scale counts of each of several geographically arranged groupings. He indicated the ranges by vertical lines on which the means were located by symbol according to sex. The means were connected so as to portray the variational trends (now called clines). This presentation was useful and promising, but failed to indicate the significance of the observed differences or to give more than the crudest idea of the degree of overlap or separation between samples.

A valuable and clever addition to Ruthven's format was proposed by Dice and Leraas (1936). In each vertical line showing the range and the mean for a sample they inserted a rectangular bar, like those in Figure 1, outlining two standard errors of the mean ($2\sigma_M$) on either side of the mean. This method was designed to indicate and to test the significance of the difference between the means of each pair of samples portrayed. It was shown that the level of "significance" arbitrarily adopted by biologists was just about satisfied when two rectangles met, end to end, on the same horizontal.

Following the same lead, Hubbs and Perlmutter (1942) pointed out that "this is a special case; we need some indication too of the significance of the differences (t values), corresponding to the varying relative lengths, and to the varying overlap or separation, of the rectangles." Though many biologists and some statisticians still accept such an arbitrary distinction, there is no magic line (as $P=$ .05 or .01), where totally unreliable evidence suddenly gives way to completely trustworthy indications of significant difference (see Figure 4).

With the aid of biometrician Charles W. Cotterman, Hubbs and Perlmutter indicated in tabular form just what degree of reliability can be attributed to data showing, when graphed as in Figure 1, varying degrees of overlap or of separation between the bars outlining $2\sigma_M$ on either side of the mean. They concluded

> that considerable reliance can be placed on the significance of the difference between samples, if the corresponding rectangles are only slightly separated, or if the overlap is not more than about 33 per cent of the length of the shorter of the two rectangles. When the longer rectangle is 2 to 4 or more times as long as the shorter one, an overlap of 50 per cent or even 75 per cent does not negate the probability that a significant difference exists. If the gap between the rectangles exceeds 10 per cent of the length of the shorter, the significance of the difference between the populations may be regarded as demonstrated beyond any reasonable doubt (if we assume the samples to be representative).
>
> When the overlap of two subequal rectangles exceeds one third of the length of the shorter rectangle, little or no reliance can rightly be placed on the significance of the difference. When the overlap is 50 per cent the odds of significance are less than 10 to 1 unless the length of one rectangle is more

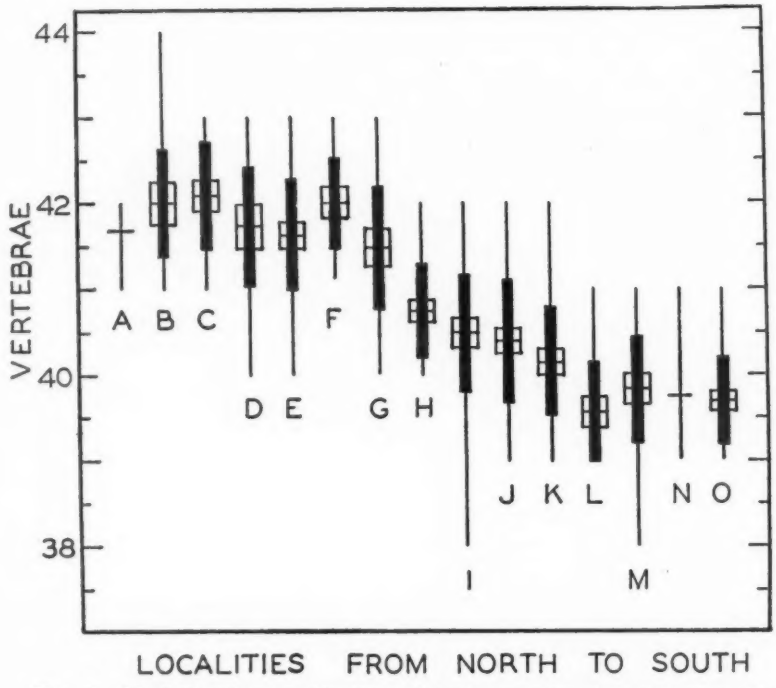


FIG. 1. Variation from north to south in the number of vertebrae of the anchovy, *Anchoviella mitchilli*.

A, Massachusetts (3 specimens); B, Great Peconic Bay, New York (25); C, Hudson River, New York (50); D, Great South Bay, New York (30); E, New Jersey north of Cape May (63); F, Cape May, New Jersey (30); G, Mount Landing, Virginia (48); H, Charleston Harbor, South Carolina (77); I, Georgia (64); J. eastern Florida (95); K, western peninsular Florida (77); L, St. Andrews Bay, Florida (50); M. Texas (47); N, Río Papaloapam, Mexico (8); O, Yucatán (100). See text for a description of the graph.

FIG. 1. Reproduction of figure presented by Hubbs and Perlmutter (1942) to illustrate their modification of the Dice and Leraas method for the graphical comparison of series of samples. Subsequent workers have portrayed the standard deviation (σ) on either side of mean as a narrow hollow bar.

than 4 times that of the other. Such differences in the values for σ_M are very rare in comparable data. Ordinarily any very considerable overlap renders the significance of the difference very doubtful.

Hubbs and Perlmutter further modified the graphical method by adding to the diagram for each sample (see Figure 1) a measure of dispersion (σ, the standard deviation). This parameter nicely supplemented the measure of reliability ($2\sigma_M$) introduced by Dice and Leraas. The distinction between these two measures, though still far from being universally appreciated, is of great importance. The standard deviation measures dispersion about the mean. Its values, except for fluctuations induced by very small samples, do not vary with the size of the sample. The values for σ_M, on the contrary, bear on the reliability of the data and vary inversely with the square-root of the number of variates. Hubbs and Perlmutter noted:

> When two samples showing normal variation are compared, an overlap in the frequencies of about 16 per cent only is indicated when the broad bars representing the standard deviations neither overlap nor are separated on the ordinate scale. That is, about 84 per cent of the specimens of both categories would then be separable, in that their values for the given character would lie on the proper side of the line best separating the two populations. Such differences are approximately of the order that may be utilized for subspecific separation.

A number of authors, representing botany and paleontology as well as several fields of zoology, have utilized the graphical method successively elaborated by Ruthven, Dice and Leraas, and Hubbs and Perlmutter. Some, as Hubbs and Hubbs (1947), Pitelka (1950), Tordoff (1952), and Storer (1952), have modified the drafting format. It became apparent that the use of a hollow instead of a black bar to embrace σ on either side of the mean was necessitated by the circumstance that at times the value for σ transgresses in one direction the observed range. Ordinarily, the bars representing $2\sigma_M$, or this value and σ, on either side of the mean, have been drawn, more or less as in Figure 1, awkwardly straddling the line indicating the range of variation; and the lines have been kept vertical by most authors.

When confronted with the need of presenting by some such method a large amount of data, in part involving long series of samples, the junior author found

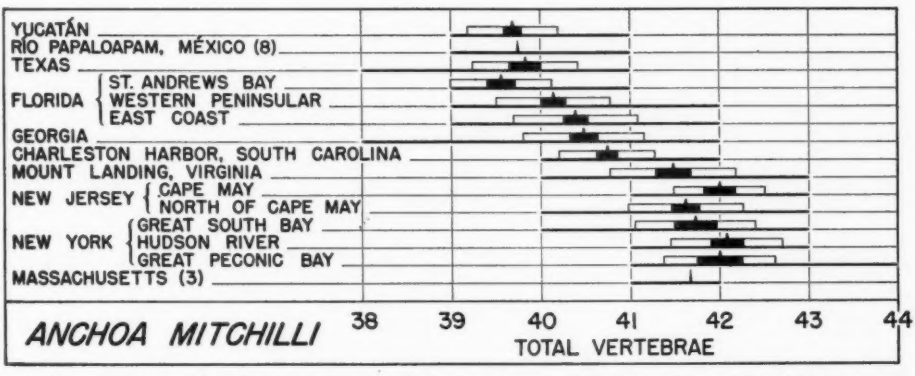


FIG. 2. Regraphing by new format of the same data shown in Fig. 1. Drafted by Robert W. Kirk. The guidelines are very helpful but not essential. For each locality the range of variation is shown by a heavy horizontal line; the mean (M), by a small, narrow triangle. The blackened part of each bar comprises 2 standard errors of the mean ($2\sigma_M$) on either side of M. One-half of each black bar plus the white bar at either end outline 1 standard deviation (σ) on either side of M. σ indicates dispersion; 2 σ_M, reliability.

the previously used graphical techniques time-consuming and in some ways inadequate. The authors together then reconsidered the mode of presentation and arrived at a simple and, we think, otherwise better format. The modified method, which presents the same parameters that were graphed by Hubbs and Perlmutter, has been used by the junior author repeatedly in his recent monographs (Hubbs, 1952 and 1953) on the clinid fishes and in other contributions in press, and has been adopted by the senior author in several papers now in preparation. Through personal contacts some publicity has been given to the improved method.

The differences between the two drafting techniques become evident on comparing Figure 1 (Hubbs and Perlmutter's test case) with Figure 2, which presents the same data much more simply. The basic differences lie in the elimination of a useless half of each bar and in the horizontal alignment of each diagram. Oliver (1948, p. 180) also used the unilateral form on a horizontal basis, but did not include the bar for σ.

Following are advantages of the method:

1. The horizontal alignment (*a*) facilitates comparisons, (*b*) renders more facile and satisfactory the inclusion on the graph of such data as the localities given on Figure 2, and (*c*) is more quickly grasped, because it is conventional in presenting such data by frequency tables or graphs, and somewhat suggests a frequency curve.
2. The data are more compact. The vertical space occupied by the new graph, per unit of width, is 45 per cent of that of the prior graph, or only 36 per cent if account be taken of the inclusion within the new format of the geographical data that required a long sublegend in the old. Twice as many samples can be compared in a full-page graph.
3. The drafting is easier, in that each unit requires only 7 lines (or 6 lines plus a small triangle quickly made with the templet for W on a lettering guide), instead of 10 lines, and has fewer close-set parallel lines, slight misplacements of which are glaring.
4. The simpler bars facilitate the recognition of σ and of $2\sigma_M$ and render more apparent the degree of overlap, or separation, of the bars.
5. The darkening of the central (standard-error) bars emphasizes the values that most often call for comparison.
6. The greater simplicity adds to the attractiveness of the diagram.
7. The new graphical method allows two diagrams to be drawn on either side of a line (one up and the other down, or one to left, the other to right), as for expressing fluctuations of proportions at several different lengths of a fish.

Usually the bars covering $4\sigma_M$ will be blackened in, but occasionally, as when superimposed over a scatter diagram, the bars will need to be stippled, cross-hatched, or otherwise shaded, so as not to conceal underlying symbols. When several sets of data are repeated on the same graph, it may be desirable to identify all diagrams pertaining to the same series (or species) by a distinctive type of shading. Such a graph could have several clusters of diagrams, in each of which one diagram would have the standard-error bar stippled, another cross-hatched, another stippled, and so on.

An innovation in Figure 2, the light guidelines, will facilitate examination and will often eliminate the need for using a square to determine whether or how much the bars of distant units overlap or are separated.

Through representation by a heavy line, now at the bottom of each unit, the range can be made to stand out even when it happens to be overlapped on one side of the mean by the outer (white) part of the bar representing σ, or even (in very ex-

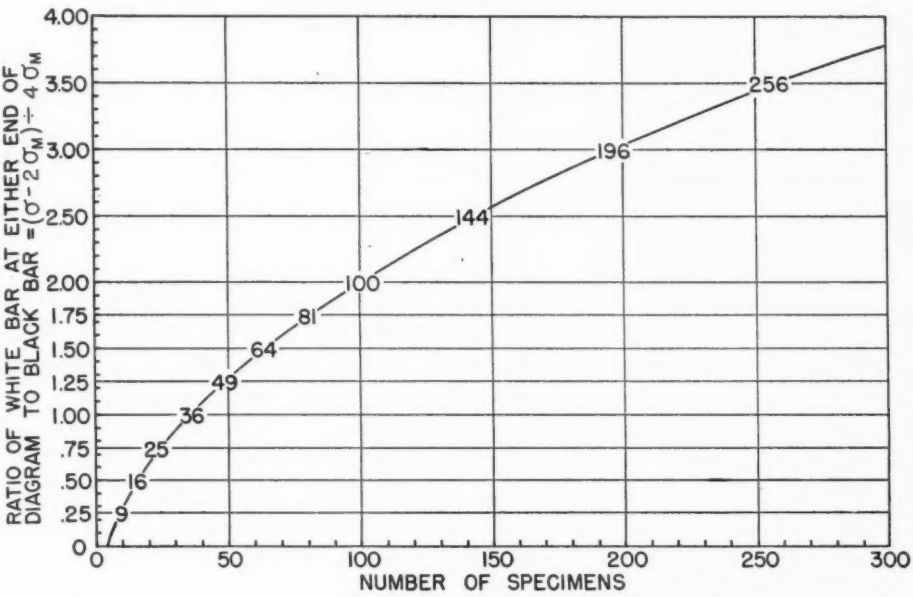


FIG. 3. Data for estimation of number of specimens in each sample from graphs like Fig. 2. Drafted by Robert W. Kirk.

ceptional cases) by the dark bar portraying $2\sigma_M$.

Some authors have indicated on their graphs the number of specimens for each sample. This could have been done in parentheses following the legends on the left side of Figure 2. It is hardly necessary, however, to specify the numbers, for if we keep in mind the numerical relationship between σ and $2\sigma_M$, we can by inspection of the graph approximate the number of specimens in each lot. The difference is proportional to that between N and $2\sqrt{N}$. Thus, if there are 4 specimens, the two bars of the diagram will coincide, since $4=2\sqrt{4}$. For the simplest visual estimate of the number of specimens we may compare the ratio in lengths between the white bar at either end of each diagram in Figure 2 ($\sigma-2\sigma_M$) and the entire dark bar ($4\sigma_M$). It can readily be computed that the sample comprises 9 specimens when the white bar is one-fourth as long as the dark bar; 16 when one-half as long; 25 when three-fourths as long; 36 when of equal length; 49 when one-fourth longer; 64 when one-half longer; and so on. These values are indicated on Figure 3, which allows for ready interpolation. When the values for σ have been rounded off, the estimates of number of specimens lose some precision, but are sufficiently accurate.

Since for most purposes the statistical parameters vary little for samples of more than 30 specimens and remain nearly constant for samples of more than 100, graphs constructed in the style of Figure 2 indicate at a glance that statistical adequacy is approached when either white end-bar exceeds the dark bar in length, and is ordinarily fully attained when the white bar is more than twice as long as the dark. When the white bar is much shorter than the dark, the values for that sample cannot be regarded with much confidence. It is recommended that only the range and the mean be indicated when 9 or fewer

specimens are involved and when, as a result, the length of the white bar would be only one-fourth, or less than one-fourth, the dark one. For such entries the number of specimens may be indicated on the graph.

When the samples include fewer than 30 specimens there are other reasons for distrusting the reliability of the difference that is indicated by the graphical method. The values for σ are calculated on the assumption of normal distribution, not likely to be realized in small samples, and the values for t (considered below) are calculated by the conventional large-sample formula (as indicated by Hubbs and Perlmutter). For comparisons of small series, statitisticians favor a formula designed for such samples, such as the "Student" t test. For especially critical comparisons of samples having fewer than 30 specimens, the use of such a formula is recommended.

Since the length of the dark bar and its limits are of critical significance in the graphical interpretation, the drafting should be precise, and the outer edge of the bar to be inked in should be run on the exact limit.

The criticisms levied against the Dice-Leraas method by Simpson and Roe (1939, pp. 316-320) would apply with equal force against the proposed modification, but were answered, we think adequately, by Hubbs and Perlmutter. We regard the method as sufficiently valid and precise for most biological applications. With the inclusion of a bar to represent the standard deviation (σ), but not of the often transgressed "theoretical ranges ($M \pm 3\sigma$)" proposed by Simpson and Roe, the method, especially when graphically refined as here proposed, provides an adequate means of publishing data that would be less readily understood and very space-consuming and cumbersome to present in tabular form.

We now offer in one graph (Figure 4), rather than in two tables, as Hubbs and Perlmutter did, an improved means for determining, very quickly and without any involved calculations, the probable significance of the observed differences between any two samples in a series plotted as in Figure 2. The graphical analysis follows a simple procedure. First, one estimates roughly (for high precision is unnecessary and hardly justified) the ratio of the lengths of the two pertinent dark bars, each representing $4\sigma_M$. This estimate can be made rather adequately by mere inspection; better by stepping, with dividers, the shorter dark bar into the longer. From the ratio thus obtained one selects the appropriate straight line as labeled on the right margin of Figure 4, or interpolates between two of these lines. Next, one estimates approximately —visual inspection or a quick manipulation of the dividers suffices—the overlap or separation of the two bars, expressed as a percentage of the length of the shorter bar. Then, from the ascertained percentage scaled on the lower margin one reads up to the chosen straight line, or point of interpolation, and on the horizontal thus located reads off, on the left margin, the approximate and sufficiently precise t value (the ratio of the difference between the means to the standard error of this difference). The odds of significance corresponding to certain t values, also recorded on the left margin, give an approximate idea of the significance of the difference. To obtain the value of P (the conventional expression of the probability that the observed difference is due to chance), one follows the horizontal line, located as indicated above, to the heavy line labeled P and reads off the corresponding P value as scaled along the upper margin. If one prefers to think in other terms, it is possible to compute quickly the odds of significance from the formula $(1-P) \div P$.

The graphical analysis rendered by Figure 4 makes it clearly obvious why a broad overlap of the dark bars indicates low reliability of the observed difference between two samples and why any considerable separation of these bars indicates a high reliability. The sloping lines

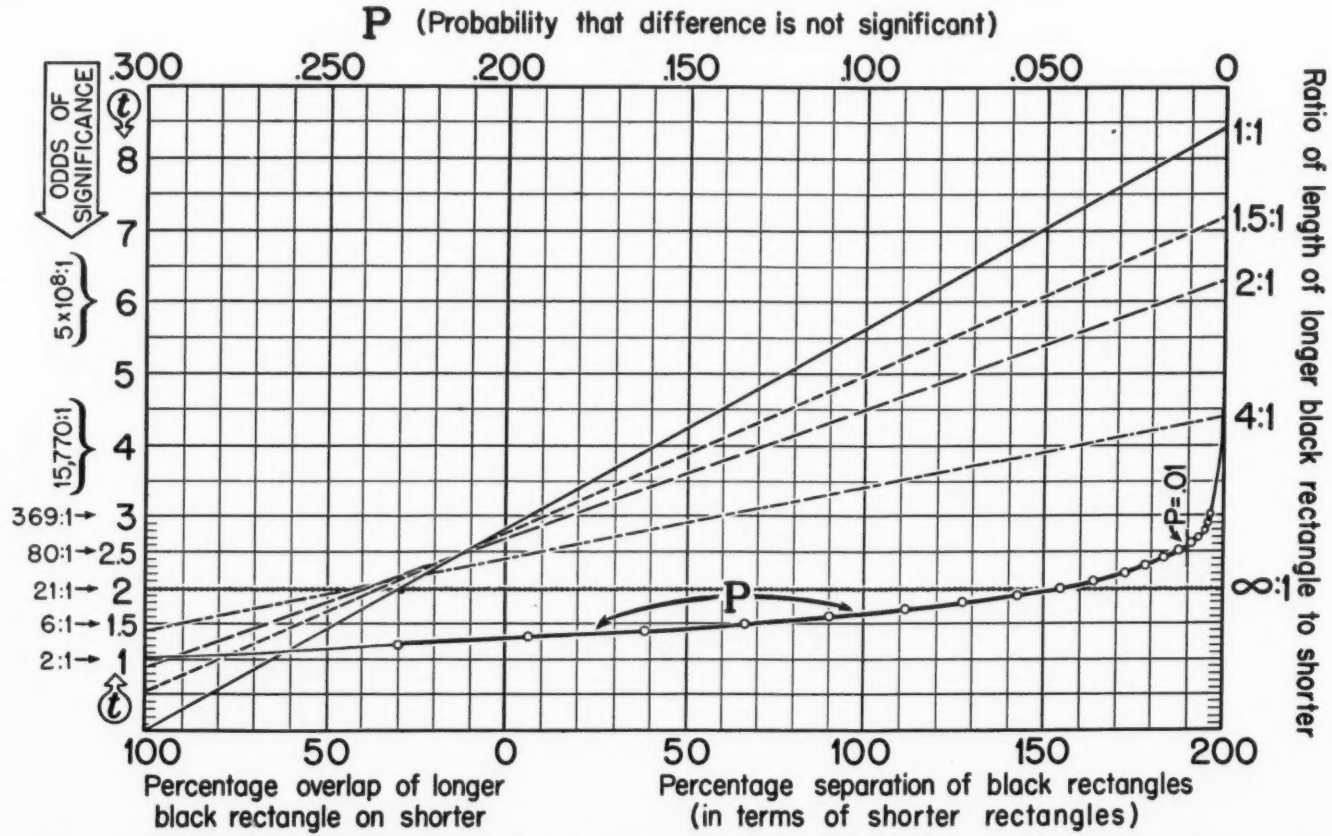


FIG. 4. Graphical analysis of the difference between any two samples graphed in the style of Fig. 2. Prepared from data presented by Hubbs and Perlmutter (1942, Tables I and II). Drafted by William L. Brudon. The straight lines are read against the left margin and the bottom of the graph; the heavy *P* line, against the left margin and the top. For procedure in using graph, see text.

representing the ordinary fluctuations in the relative lengths of the two dark bars intercept the vertical line of neither overlap nor separation (0 on the graph) at points corresponding with the narrow region where the *P* curve is very abruptly inflected.

A word of caution may be intercalated regarding the degree of confidence to be placed in the measures of reliability, especially when the values for *t* are very high (or those for *P* are very low). The computations of these measures are based on assumptions, including the normal distribution of variates, that may not be completely justified. All such computations are subject to fluctuation and should be treated as approximations. High values of *t* are trustworthy and low values unreliable, much as is indicated in the preceding discussion, but not to the exact degree indicated. The probability of divergent samples in biology representing similar populations is likely to be rather greater than is indicated by the conventional computations, for the frequency curves tail out on either side more extensively than would be indicated by the statistical theory. The chances of unusual values unexpectedly appearing are often greater in biological than in other data, because of the complex factors involved.

When used with reasonable reserve, however, the methods here presented for the graphical analysis and comparison of series of samples are highly efficacious and economical and are adequate for most purposes in systematics and other fields of biology. These methods permit rapid and comprehensive comparisons; well portray similarities, differences, and trends; and indicate with sufficient precision the degree of divergence between samples and the reliability of the indicated distinctions. Ordinarily, higher precision is not needed, and, indeed, is often unjustified.

Addendum

The method proposed by Hubbs and Perlmutter has been presented by Mayr, Linsley, and Usinger in their book on the *Methods and Principles of Systematic Zoology* (McGraw-Hill Book Co., 1953; pp. 142-150, Fig. 26). They suggest, however, the plotting of 1.5σ on either side of the mean, instead of 1.0σ, in order "to indicate probable subspecific difference" by a non-overlap of the bars. Neither overlap nor separation of the bars representing 1.5σ would indicate, with normal distributions, the separability of 93 per cent of the specimens. The same authors, however, elsewhere recommend a value of 1.28σ as indicating "the conventional level of subspecific difference" (90 per cent separation). Both values seem higher than those usually accepted (0.675σ and 75 per cent). Our recommended plotting of 1.0σ on either side of the mean, indicating an 84 per cent separation, seems to us quite adequate.

In view of the obvious advantages of plotting the data recommended by Hubbs and Perlmutter, we disagree with the indication by Cazier and Bacon, in the "Introduction to Quantitative Systematics" (*Bull. Am. Mus. Nat. Hist., 93,* 383-384, Fig. 12), that for usual systematic purposes it is sufficient to plot the mean, the observed range, and the "calculated range" (3σ).

REFERENCES

DICE, L. R., and LERAAS, H. J. 1936. A graphic method for comparing several sets of measurements. *Contr. Lab. Vert. Gen. Univ. Mich.,* No. 3.

HUBBS, CARL L., and HUBBS, LAURA C. 1947. Natural hybrids between two species of catostomid fishes. *Pap. Mich. Acad. Sci., Arts, and Letters, 31* (1945), 147–167.

HUBBS, CARL L., and PERLMUTTER, A. 1942. Biometric comparison of several samples, with particular reference to racial investigations. *Am. Naturalist, 76,* 582–592.

(*Concluded on p. 92*)

Regularity of Form in Organisms

MICHAEL M. NOVIKOFF

ONE of the most interesting and important problems of comparative anatomy is the multiformity and at the same time the regularity of the shapes in the structure of plants and animals. Richard Owen, the eminent British zoologist, had in the past century proposed two principles for comparing the organs and appendages of different animals. The first of these, *analogy*, characterizes the physiological likeness of organs which perform similar functions, and hence often assume similar shapes, as for instance, the wings of birds and of bats. The second principle, *homology*, is concerned with organs which, although fundamentally similar in structure, may be different both in form and in function, such as the syringe hole in whales and the nose of other vertebrates.

K. Gegenbaur, in his enthusiasm about Darwin's theory of evolution, came to the conclusion that comparative anatomy should be based on the historical method, that is, should study the gradual development of the animal kingdom. Proceeding from this conclusion, he described as homologous such parts of the body as have been derived from a common ancestor and, consequently, are characterized by blood relationship, although they may differ in appearance and shape, as for instance the appendages of the various vertebrates (fishes, birds, mammals). The principle of analogy, however, Gegenbaur declared superfluous for the purposes of comparative anatomy, as having no bearing whatever on the evolution of organisms.

By restricting in this way the methodology of comparative anatomy Gegenbaur at the same time also limited the material eligible for comparative study. In common with most of his followers he began to deal almost exclusively with the vertebrates in which the symptoms of homology stand out with exceptional clearness.

As this limitation of the very matter and scope of comparative anatomical research seemed unjustified, I have endeavoured to show that analogy is manifest in living nature, in a variety of ways, much more frequently than had hitherto been believed, and that the parallelism observable in the structure of numerous organs in different groups of animals expresses a principle far broader than the principle of homology. The inexhaustible variety of forms apparent in the representatives of the marine fauna makes it clear that the method of limiting comparative anatomical research to the insignificant (from the morphological point of view) group of vertebrates is entirely wrong. On the other hand, if we extend our comparative study of various organs to the whole of the animal realm, we come to the conclusion that most organs exhibiting parallelism are found in forms which are phylogenetically unrelated.

Parallelism of form can be observed in various systems of organs. The regularity is most clearly revealed in the shapes of shells and in the structure of organs of photoreception (Figs. 1, 2). Shells and other protective structures are found in widely divergent groups of the animal kingdom—in Protozoa, Polychaeta, Trichoptera, Lepidoptera, Pteropoda, Gastropoda, and Cephalopoda (Fig. 1). They are built from a variety of materials, such as chitin, calcium carbonate, and silica. Moreover, in some cases these substances are secreted by the entire surface of the animal, in other cases by a special mantle, that is by a portion of the body, and in still others (insects), by a few small glands opening at the anterior end of the body. Yet, in unicellular and multicellular forms alike, the protective coverings invariably take the following three typical shapes:

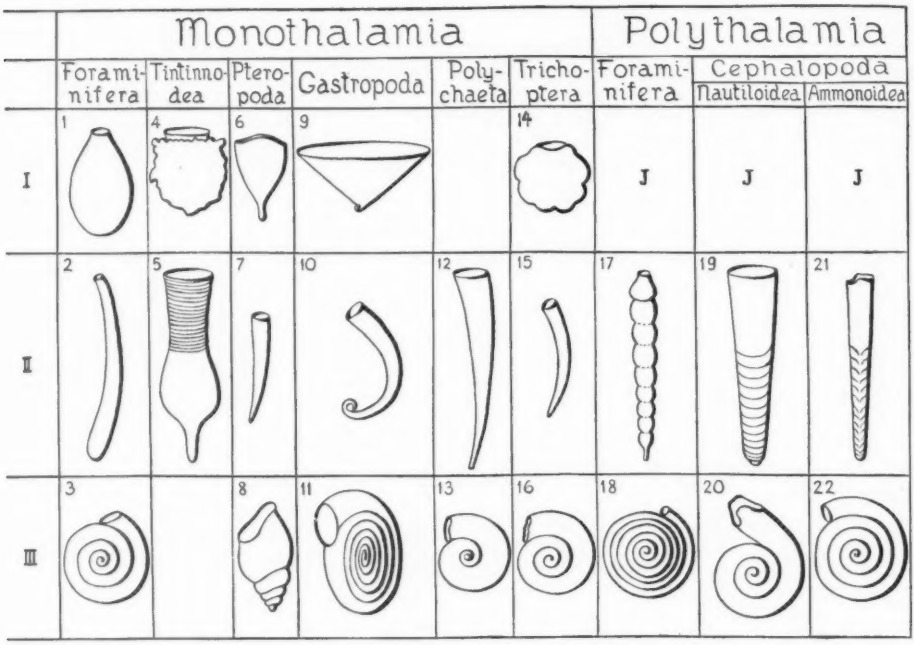


FIG. 1. Shells. I, cup-like; II, tubular; III, spiral. 1, *Gromia oviformis;* 2, *Hyperammina elongata;* 3, *Ammodiscus tenuis;* 4, *Tintinnopsis ventricosa;* 5, *Codonella orthoceras;* 6, *Clio balantium;* 7, *Creseis virgula;* 8, *Spirialis bulimoides;* 9, *Patella* sp.; 10, *Cyclosaurus Mariei;* 11, *Polygyratia* sp.; 12, *Pectinaria auricoma;* 13, *Serpula spirulaea;* 14, *Rhyacophila* sp.; 15, *Leptoceras* sp.; 16, *Helicopsyche sperata;* 17, *Nodosaria hispida;* 18, *Spirillina vivipara;* 19, *Orthoceras timidum;* 20, *Ophidioceras simplex;* 21, *Bactrites elegans;* 22, *Arietites bisulcatus. J,* the first chamber of the shell.

cups, tubes, and spirals. These basic forms occur in all of the groups mentioned except the polychaetes, whose elongated bodies naturally preclude the possibility of formation of a cup-shaped shell. The recurrence of these three shell shapes illustrates the inherent morphogenetic regularity which prevails in the various groups of the animal kingdom. We can assert that living matter is capable of producing but a small or, more accurately, a limited number of fundamental forms, while the vast number of existing varieties results from all possible modifications and combinations of the basic forms.

This tendency for basic structural patterns to recur in unrelated groups of animals is still more evident from an examination of the organs of photoreception. In all the phyla of the animal kingdom (with the exception, of course, of Protozoa) four principal types of eye structure are observed, in which the eyes are provided respectively with (1) a flat retina, (2) a cup-shaped retina, (3) a vesicular retina, and (4) a convex retina (Fig. 2). The last-mentioned type is ordinarily called a compound eye. It is noteworthy that the coelenterates, which are provided with well-developed eyes of the first three categories, lack the especially complex organs of the fourth type. The compound eye, it is true, is not characteristic of either Echinodermata or Chordata; yet in some representatives of each of these phyla there is a clearly manifest, though incompletely expressed, tendency for the formation of these complex organs (e.g., oculars of sea-

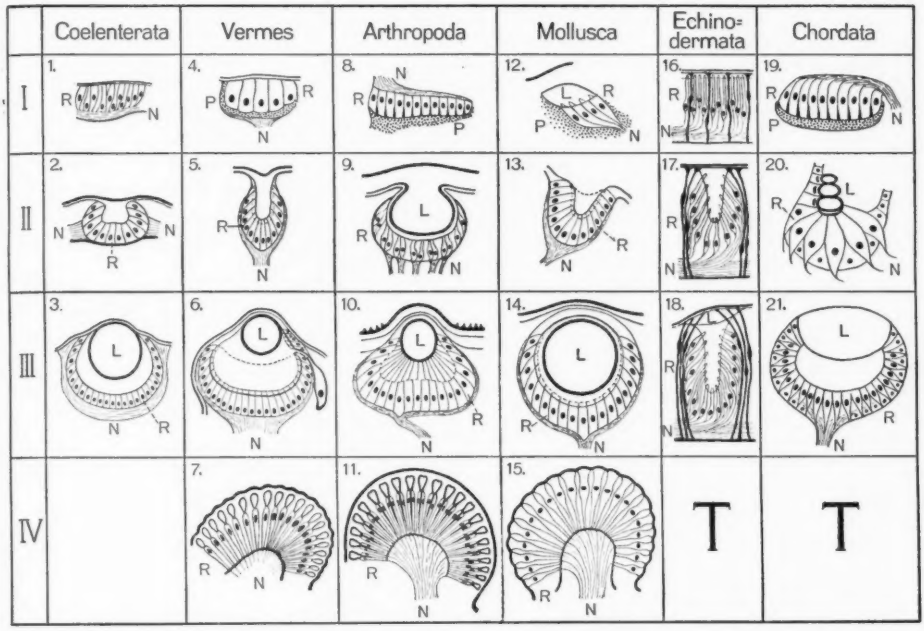


FIG. 2. Organs of photoreception. I, flat eyes; II, cup-shaped eyes; III, vesicular eyes; IV, convex (compound) eyes. 1, *Aurelia aurita;* 2, *Sarsia mirabilis;* 3, *Charybdea marsupialis;* 4, *Nais proboscidea;* 5, *Ranzania sagittaria;* 6, *Vanadis formosa;* 7, *Sabella reniformis;* 8, *Limnadia lenticularis* (one ocellus of the median eye); 9, *Limulus polyphemus;* 10, *Peripatus Edwardsii;* 11, *Limnadia lenticularis* (compound eye); 12, *Chiton subfuscus;* 13, *Patella* sp.; 14, *Murex* sp.; 15, *Arca Noae;* 16, *Astropecten Mülleri;* 17, *Astropsis pulvillus;* 18, *Asteria tenuispina;* 19, *Salpa pinnata* (one ocellus of the complex photoreceptive organ); 20, *Amaroucium constellatum* (larva); 21, *Lacerta agilis* (embryo—pineal eye). *T*, tendency toward formation of a compound eye; *L*, lens; *N*, optic nerve; *P*, pigment; *R*, retina.

stars and complicated eye-groups of salps). This tendency is designated in Figure 2 by the letter *T*. Comparative study of central nervous systems, locomotor appendages, and luminescent organs reveals a similar recurrence of basic structural pattern for each organ or system, wherever it occurs in the animal kingdom (Novikoff, 1930).

Shortly after the publication of my book entitled *Das Prinzip der Analogie und die vergleichende Anatomie,* Prof. B. Nemec (1931), of the University of Prague, showed that in the plant kingdom, too, regular parallelism of form is a characteristic phenomenon. Furthermore, in his book *Organismi e Vita* (1935), Prof. G. Colosi lists a number of interesting examples of parallelism in phylogenetically unrelated organisms. These examples included both animals and plants. Further corroboration of my views is contained in *Das Gefüge des Lebens* by Prof. L. von Bertalanffy (1937). In a recent book entitled *Entwicklung als grundgesetzliche Notwendigkeit* (1948) Prof. H. Krieg of Munich expresses agreement with my conclusions.

Further research work in this field, however, has led me to believe that the concept of analogy includes two different categories of phenomena. One clearly corresponds to the accepted definition of this term, according to which analogous forms are understood to be those that have been secondarily acquired by animals or plants

in adaptation to similar environmental situations. As an appropriate example of such an analogy one may cite the front appendages of such widely different animals as the mole, *Talpa europaea,* and the mole cricket, *Gryllotalpa vulgaris.* The ends of the front legs of both the mammalian burrower and the insect burrower are shovel-like, well suited to digging underground. Another example, the acquisition of a snow-white fur or plumage by various animals of the northern regions, may be mentioned. This analogy is concerned with a purely physiological phenomenon and is therefore in contrast to homology, which is a morphological or phylogenetic phenomenon. However, these two principles of comparative study, namely, physiological analogy and phylogenetic homology, are far too inadequate to cover the vast variety of parallel forms apparent in nature. In the tabular classifications mentioned above, there are to be found, together with examples of analogy and homology, striking similarities in organ structure which cannot be explained either by close kinship of the animals bearing them or by the physiological role played by the organ. Clearly, the shape of shells (in both unicellular and multicellular animals), which are organs of a purely passive nature, cannot be attributed to either cause.

Typical analogy is comparatively rare in the animal kingdom, a circumstance which, among other reasons, apparently induced Gegenbaur to abandon this principle as a method of research in comparative anatomy. There is, however, another kind of parallelism of organic structure which is much more frequently encountered, and which was formerly considered a category of analogy. This parallelism is not of a secondary nature, as is analogy, but represents a primary morphological phenomenon which has its origin in the fundamental morphogenetic capacities and limitations of living matter. It is therefore dependent chiefly on the internal properties of organisms, that is, on those highly complex reactions which take place, on the one hand, between the component parts of the organism and, on the other hand, between the organism and its environment. For this third kind of parallelism, as distinct from both analogy and homology, I have proposed the term *homomorphism* or *homomorphy.*

The principle of homomorphism has a certain relation to the term "orthogenesis" introduced by Eimer. Both phenomena are dependent on the properties of the organism itself and not on those of its environment. But orthogenesis designates the tendency of organisms to develop phylogenetically in a definite direction, whereas the essential point of the concept of homomorphism is that the representatives of widely separated phyla of animals and plants possess similar organs which have undergone parallel evolution. Thus regularity of form arises independently both of blood relationship and of environment.

From the point of view of genetics we can best conceive of the difference between the three kinds of parallelism in the following manner. Homologous organs are formed through basically similar developmental processes controlled by gene complexes somewhat modified from that of their common ancestor. Thus, when considering the appendicular skeletons in different classes of vertebrates, it can be assumed that the set of genes which controls the development of the fin of a bony fish, the wing of a bird, or the leg of a mammal has each *diverged* in the course of time from the set of genes which controlled the development of the fin in their common piscine ancestor. In physiological or functional analogy, on the other hand, sets of genes in wholly unrelated organisms, which control radically different developmental processes, are altered in the course of time so that the function and shape of the resulting organs *converge.* Thus, in the example of the mole and mole cricket, the entirely different sets of genes controlling the development of the insect leg and the mammal leg have been much modified from their respective ancestral conditions as the phenotypes were selected to perform similar functions. The nature of the hereditary basis of homomorphic similarities is more difficult to comprehend. The possibility might be

considered that even in very dissimilar phyla, organisms have sufficient genes in common so that the selection of *parallel* mutations might produce phenotypic similarities. As a result, organs of identical form would be found in representatives of different phyla. It is, however, difficult to believe that the eyes of animals so dissimilar as coelenterates, arthropods, and chordates, could be controlled by homologous genes. And yet there is a striking resemblance among these organs, both in general form and in details of structure.

The phenomenon of homomorphism cannot be directly connected with function nor with adaptation to the environment: many homomorphic organs appear not to play similar roles in the economy of the animals that bear them. Thus, we can easily comprehend the necessity for the complex structure of the compound eyes of insects, the functional perfection of which is in marvelous harmony with the rapidity of flight in these animals. Less comprehensible from the physiological point of view is the perfection of the same kind of eye in the crayfish which habitually lives in semidarkness and moves much more slowly than most insects. But it is quite incomprehensible why in certain almost motionless molluscs, as for instance *Arca Noae,* several hundred equally elaborate compound eyes should have developed on the edge of the mantle. As the stimuli from these photoreceptors only effect the closing of the shell, such an arrangement appears to be too complicated, too prodigal. (Similar discrepancy between form and function is dealt with in an extensive treatise by Prof. Rabaud (1925). He cites, as an interesting example, the grasping appendages with which certain predacious arthropods catch their prey, as in the mantids; yet appendages of precisely the same shape develop in many purely phytophagous insects, to which they must be quite useless.) Homomorphism is probably a reflection of the inability of living matter to form efficient organs of specified function (photoreception, for example) in more than a limited number of ways.

Although the concepts of homology and analogy are fundamentally different in principle, in practice it is often difficult to determine with which one we are concerned. Sometimes it is even more difficult to decide whether a given phenomenon should be classed as homomorphous or as belonging to one of the other two categories of parallelism. It may be said that the chief factor in homology is of a phylogenetic, in analogy of a physiological, and in homomorphism of a purely morphological nature.

In the charts which I have prepared to illustrate the general morphogenetic regularity of development, the phenomena of homology, analogy, and homomorphism are not grouped under separate headings, but the last-mentioned category undoubtedly predominates. This can be shown more clearly by the following example. Under the influence of the brilliant success of Darwin's theory of evolution, an attempt was made to classify the compound eyes in annelids, molluscs, and arthropods as homologous organs, alleging the descent of these three phyla from a common ancestor. However, the careful investigations by Plate (1922) have made it abundantly clear that these organs of sight—even within the arthropods alone—could have been derived from three or four different ancestral types. In my opinion, this is a clear indication that these organs are homomorphous.

In my introductory remarks I mentioned that Gegenbaur had limited comparative anatomical research solely to the historical aspect. The method of investigation of homomorphism is quite different, as it involves the classification of organic forms in accordance with their basic spatial patterns. This I have called the "typological" method. It could be said that the study of homology is chiefly concerned with the concept of time, while that of homomorphism is concerned with space.

There is another purely formal consequence of the introduction of the "typological" method into comparative anatomical research. The historical method recommended by Gegenbaur and his school is practicable chiefly within the limits of cohesive, more or less extensive, groups

of animals. Within these limits, admittedly, this method has led to excellent results, as, for example, the determination of the gradual formation of the one-toed foot of the modern horse from the five-toed appendage of its fossil ancestor. The success of the "typological" method, on the other hand, is based on the fact that these investigations are not restricted to a few groups of organisms, but can extend to the entire animal (or plant) kingdom, with all the countless varieties of living and extinct forms. From this diversity typical forms are singled out to illustrate the morphogenetic regularity. This science, which concerns itself with organic form, should properly be designated as comparative morphology.

It is to be hoped that the combined application of the historical and the "typological" methods will prove useful and appropriate in comparative morphology. This will enable us to penetrate further into the mystery surrounding the origin of the various shapes of the organs in living beings, and will also contribute to the systematisation of our knowledge in regard to the inexhaustible diversity of organic forms.

REFERENCES

BACHMANN, R. 1947. Über Homomorphie. *Anat. Anzeiger, 96,* 70.

BERTALANFFY, L. VON. 1937. Das Gefüge des Lebens. Leipzig.

COLOSI, G. 1930. Il principio dell'analogia in anatomia comparata. (A proposito di un' opera di M. Novikoff.) *Bolletino di zoologia.*

——— 1935. Organismi e Vita. Milano.

——— 1945. La dottrina dell' evoluzione e le theorie evoluzionistiche. Firenze.

EIMER, TH. 1888–1901. Die Entstehung der Arten. Jena.

GEGENBAUR, K. 1898–1901. Vergleichende Anatomie der Wirbeltiere, mit Beruecksichtigung der Wirbellosen. Leipzig.

KRIEG, H. 1948. Entwicklung als grundgesetzliche Notwendigkeit. Stuttgart.

NEMEC, B. 1931. Remarks on the principle of analogy in plants. (Czech) *Travaux scient. de l'Univ. russe de Prague, 4,* 243–253.

NOVIKOFF, M. 1927. Le parallélisme des formes chez les divers types d'animaux. *Bull. biol. de la France et de la Belgique, 61,* 25–37.

——— 1929. Das Prinzip der Analogie als Grundlage der vergleichenden Morphologie. *10th Congrès Intern. de Zoologie,* 301–321.

——— 1930. Der Parallelismus der Formen und das Programm der allgemeinen vergleichenden Morphologie. *Archivio zoologico italiano, 14,* 467–479.

——— 1930. Das Prinzip der Analogie und die vergleichende Anatomie. Jena.

——— 1931. L'anatomie comparée comme science exacte. *Comptes rendus de L'Assoc. des Anatomistes,* 1–5.

——— 1932. Les analogies dans la structure des yeux chez les animaux cordés et acordés. *Bull. intern. de l'Acad. des sci. de Bohême, 42,* 1–5.

——— 1935. Homomorphie, Homologie und Analogie. *Anat. Anzeiger, 80,* 388–392.

——— 1936. L'homomorphie comme base méthodologique d'une morphologie comparée. *Bull. de l'Assoc. russe pour les recherches scient. Prague, 4,* 1–31.

——— 1937. L'homologie et l'homomorphie considerées comme deux bases de l'anatomie comparée. *Comptes rendus de l'Assoc. des Anatomistes,* 1–6.

——— 1938. Das Studium der Homomorphien als eine wissenschaftliche Methode. *Biologia generalis.* Wien and Leipzig, *14,* 85–110.

——— 1938. General and special homomorphism. *Acta biotheoretica.* Leiden. Ser. A, *4,* 85–96.

——— 1944. Zur Frage ueber den Parallelismus im Bau der tierischen Organe, insbesondere der Augen. *Anat. Anzeiger, 95,* 118–130.

——— 1949. Zur Frage ueber das Prinzip der Homomorphie. *Anat. Anzeiger, 97,* 7–15.

——— 1949. Grundzuege der Geschichte der biologischen Theorien. Muenchen.

OWEN, R. 1843. Lectures on the comparative anatomy and physiology of the invertebrate animals. London.

PLATE, L. 1922. Allgemeine Zoologie und Abstammungslehre. Jena, vol. 1.

RABAUD, E. 1925. Les phénomènes de convergence en biologie. Paris.

This paper is the first general account to appear in English by the distinguished European zoologist who has developed the concept of homomorphism. SYSTEMATIC ZOOLOGY is honored to introduce to its readers **MICHAEL M. NOVIKOFF**, whose work, largely published in Russian, German, and French, may be known to many through textbook recounts. Dr. Novikoff, who is now in this country, has in the course of his long career been Professor in Moscow, Prague, Bratislava, and Munich, as well as President of the University of Moscow, President of the Russian Free University in Prague, and head of the Marine Biological Laboratory at Villefranche (France).

The Systematics of Vertebrate Larvae

GRACE L. ORTON

THE interpretation of the larval characteristics of the fishes and amphibians in terms of systematics and evolution presents many challenging problems. For many years, studies on early developmental stages were guided by the idea that larval characters have an ancestral, recapitulative significance, or by the belief that they are secondary adaptations with little or no evolutionary importance. Neither theory is adequate from the standpoint of systematics, and together they have somewhat hampered effective use of larval data by taxonomists. A third and more significant concept, based on principles formulated by Von Baer in the 1800s, has gained prominence in recent years through the work of de Beer and others. It emphasizes comparative studies on equivalent growth stages of different species, and provides a much sounder basis for interpreting developmental characteristics in terms of systematics and evolution.

The larval stage may serve different ecological functions in different animals. A suitably adapted larva may enable a species to succeed in a region that might otherwise be closed to it—a conspicuous factor in the distribution of many frogs. A pelagic larva may be the major dispersal stage in many marine fishes having sluggish or strongly territorial adults, paralleling a well-known life-history pattern in the invertebrates. It is often suggested that inadequate provision for embryonic nutrition is the primary factor governing the occurrence of a larval stage. Whatever the "reason" for its establishment in the ontogeny may be, the larva is subject to the operation of genetic evolutionary processes, like any other developmental stage, since all growth stages of the individual are under the control of a single genetic system.

The same basic procedures of systematics are applied to both larval and adult stages. These procedures include the analysis of variation and the study of differences and of resemblances between species and groups; and the interpretation of the basic data in terms of the primary trends of phylogeny and of secondary phenomena of adaptive radiation, convergence, "rectilinear" trends, and other patterns of evolution, at all systematic levels.

Larval Types in Fishes and Amphibians

The types of larvae that characterize different groups of fishes and amphibians differ widely in their basic characteristics, in the secondary specializations they may undergo, and in the nature of their metamorphosis.

The extant amphibians, comprising about 2500 forms, are classified in three orders (Fig. 1). In the salamanders (order Caudata) and caecilians (order Apoda) the larva is of simple structure, and differs from the adult chiefly in the gill-arch system; other larval characters are usually relatively minor and inconspicuous. In the frogs (order Salientia), larva and adult differ profoundly in many conspicuous characters, and there is a complex metamorphosis. The ecological and physiological aspects of transformation from aquatic larva to terrestrial adult in the amphibians have attracted wide attention. The emphasis on metamorphosis as an adaptive adjustment that is uniformly characteristic of the group has probably tended to divert attention from the extensive and complex differences between kinds of larvae.

In number of extant forms, fishes outnumber amphibians by perhaps 10 to 1. A very wide range of different evolutionary stocks is usually included under the

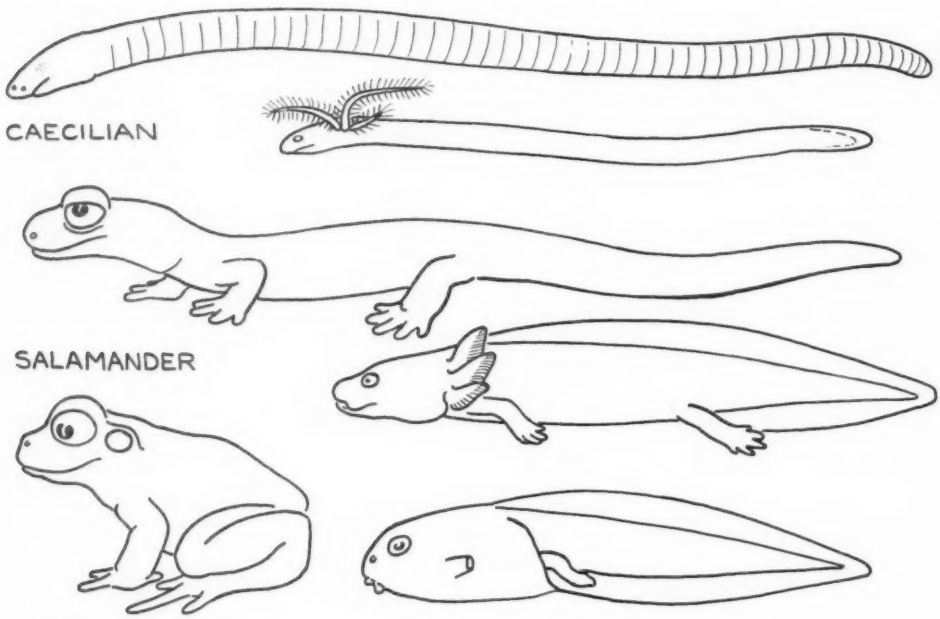


FIG. 1. Diagrams of adult and larval body form in the three orders of living amphibians.

general category of fishes—the agnathous groups, the elasmobranchs and related lines, the primitive bony fishes, including the ancestral stock of the amphibians, and the complex and diversified teleost lines. These widely divergent groups show important differences in developmental characteristics that warrant more extensive taxonomic study and interpretation.

Larval characters and their metamorphic changes present somewhat different problems in fishes and in amphibians. Fishes lack the spectacular ecological transition from water to land. Their gill apparatus and other aquatic equipment are retained throughout life, and their larval characters and metamorphic changes are usually more subtle than in the amphibians. But many fishes, particularly in the sea, do undergo a very abrupt ecological and morphological transformation from a pelagic larva to a bottom- or crevice-inhabiting adult.

There are various types of larval characters in fishes. External gills develop in the young of certain lungfishes and a few other, chiefly primitive, groups. Adhesive mechanisms are found in some newly hatched larvae, especially of fresh-water species. Many pelagic marine larvae develop some type of flotational mechanism (Fig. 2). These modifications include hypertrophied fins or finrays (*Lophius*, and many others), long spines on the body (Molidae), "ballooning" of the skin (ceratioids, some scorpaenids, etc.), or gelatinous dilution of the muscular tissue (leptocephalus larvae of eels and clupeoids). Many teleosts are characterized more by delay in development of adult form than by special larval structures. But even these species commonly have a definite and more or less prolonged larval stage (Fig. 3), characterized by distinctive early phases in the development of morphological structures and pigmentation.

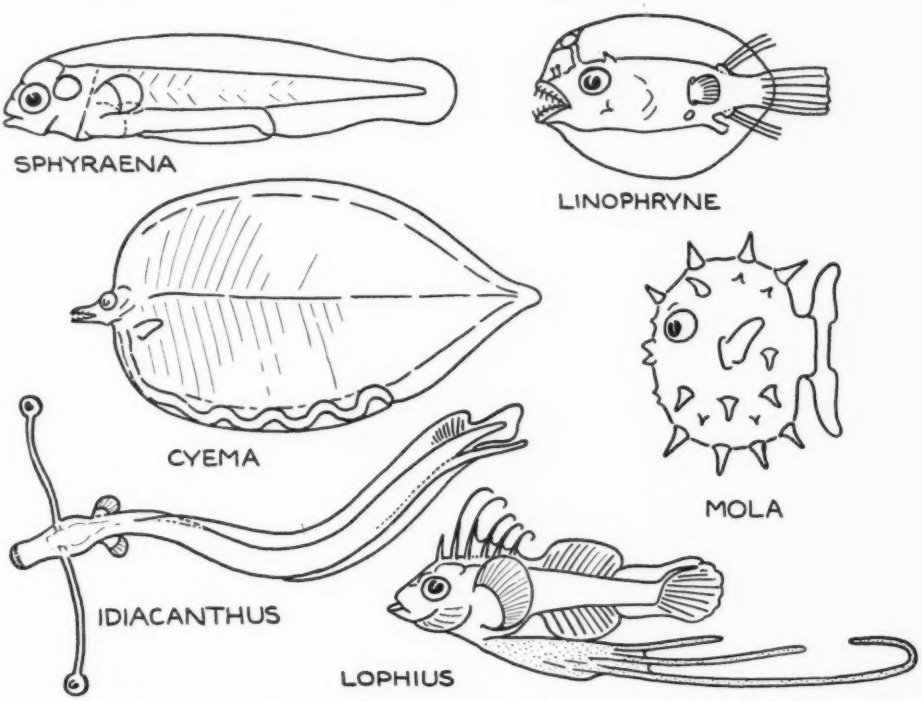


FIG. 2. Five larval fishes with specialized flotational mechanisms, and a generalized larva (*Sphyraena*, barracuda) for comparison.

Specialized types of larval fishes are sometimes designated by special names, e.g., the ammocetes larva of lampreys and the leptocephalus larva of eels and clupeoid fishes. Most of these larval names are carry-overs from the time when such forms were thought to be distinct taxonomic entities.

Specialized Patterns of Development

The addition of a free-living larval stage to the life cycle has led to many specialized types of development, including neoteny and secondary direct development. Although these two have opposite results, it is convenient to discuss them together, since the effect in each case is the more or less complete elimination of a developmental stage from the life cycle. Neoteny eliminates the former adult stage, and direct development disposes of the larva.

Neotenic animals mature reproductively while they retain some or all of the larval characters. In the salamanders, larval characters are relatively simple, and transformation involves few changes or functional interruptions that critically endanger the immediate survival of the individual. Transitional stages are not necessarily at a serious disadvantage, and indeed the neotenic species differ widely in the degree to which they complete the change from larva to adult. Furthermore, some species are neotenic only under certain ecological or physiological conditions. Neoteny is sufficiently widespread in salamanders to introduce an important complication in taxonomy. In some families all or most species transform completely, and these families are defined on the basis

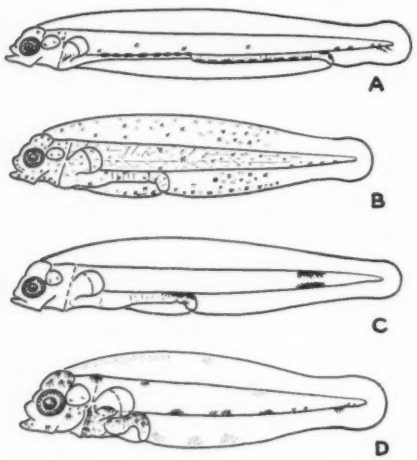


FIG. 3. Larvae of some Pacific Coast fishes showing variation in proportions and in pigmentation, characters used in the identification of larval fishes. *A*, Pacific sardine, *Sardinops caerulea*, Clupeidae; *B*, California halibut, *Paralichthys californicus*, Bothidae; *C*, Señorita, *Oxyjulis californica*, Labridae; *D*, California bonito, *Sarda lineolata*, Cybiidae.

of standard adult characters. But the several families that contain only neotenic species are necessarily defined on the basis of larval or transitional characters. When only a few such forms were known, neotenic salamanders were widely thought to be more primitive, in a recapitulative sense, than forms that undergo a normal metamorphosis. Newer understanding of the role of developmental characteristics in evolution and of the independent occurrence of neoteny in unrelated stocks has helped to clarify the classification of the main groups of salamanders.

In the frogs, metamorphosis is a critical period for the survival of the individual, for the differences between larva and adult are extreme. The changes include drastic shortening of the digestive tract and reorganization of the entire jaw region, as well as the more obvious loss of the gills and tail. Rapid completion of this vulnerable period is advantageous both to the individual and to the species. The change is probably an "all or none" process, for transitional stages are apparently incapable of feeding and are poorly adapted for prolonged survival. The apparent absence of neoteny in the frogs is perhaps associated with the extreme complexity of larval anatomy in this group.

Neoteny is apparently rare in fishes (fortunately, for the taxonomist), and it probably lacks a strong selective or competitive advantage in this highly diversified group. Since larval characters and metamorphic changes are relatively simple in most fishes, the criteria of neoteny in this group are somewhat subjective. Neoteny in fishes, as in the salamanders, occurs in various gradations and at various taxonomic levels. Certain populations of *Osmerus mordax* mature when small and transparent, only slightly if at all advanced beyond the postlarval stage; some of the small, transparent, pelagic species of gobies are neotenic; the Salangidae are neotenic salmonoids; the tiny pelagic fishes of the genus *Schindleria* are neotenic postlarvae of uncertain ordinal relationships.

In some groups that normally have a larval stage, direct development is a secondary specialization. It is widespread in amphibians, especially in the frogs, where it has appeared independently in representatives of nearly every family. In frogs that have heavily yolked eggs and terrestrial breeding habits, the larva may be more or less completely lost, in the ecological sense, but in all known examples there is still some anatomical indication of a larval stage (Fig. 4). In many of these species the embryo is a very completely equipped tadpole for a brief period. These highly modified terrestrial embryos often have useful taxonomic characters. The unique peltate gills of embryos of the "marsupial" treefrogs (*Gastrotheca* and related genera of the Hylidae) are a good example.

The two main groups of cyclostomes, the lampreys and hagfishes, differ greatly not only in anatomy but also in type of life history. The lampreys have small eggs, a

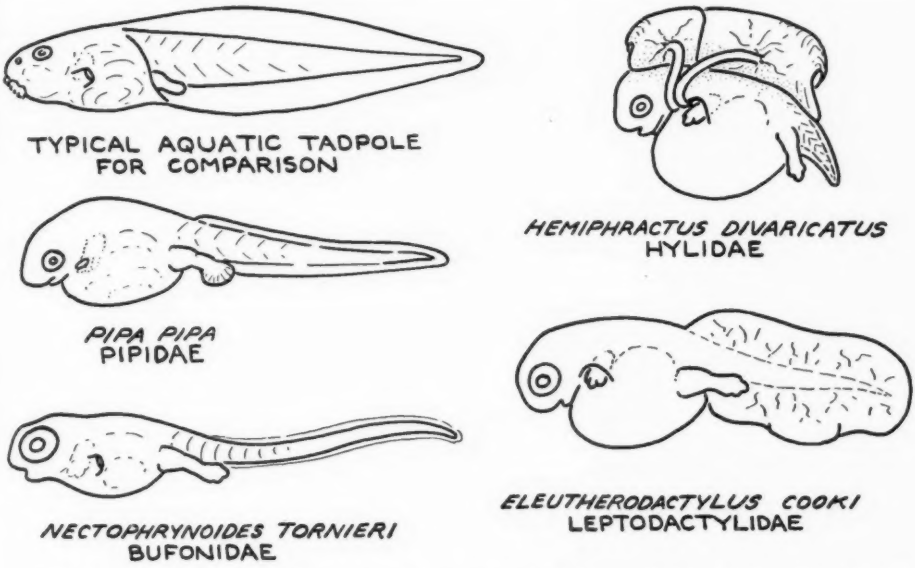


FIG. 4. Larval structures in embryos of some species of frogs that lack a free-living larval stage. Peltate gills of *Hemiphractus* form thin sheets completely enveloping embryo, but are here shown folded back to reveal gill stalks.

larval stage, and metamorphosis; the hagfishes have large eggs and direct development. With a few poorly known exceptions, the elasmobranch fishes have heavily yolked eggs or some provision for uterine nutrition, and the newborn young are relatively large and closely resemble the adults. Among the teleost fishes there is a complicated maze of developmental patterns that are greatly in need of taxonomic study. Most species have small yolk reserves and hatch in an embryonic condition (Fig. 5, upper two larvae), as do most amphibians. Other fishes have a larger yolk supply, and a greater amount of development is completed before hatching (Fig. 5, lower two larvae). The eyes and jaws may be functional and the pectoral fins present (silversides, Atherinidae); even the caudal fin and the pelvic buds may be present (flyingfishes, Exocoetidae). In some groups, notably the salmonids, not only is development far advanced at hatching, but the yolk reserve is very large and during its gradual ab-

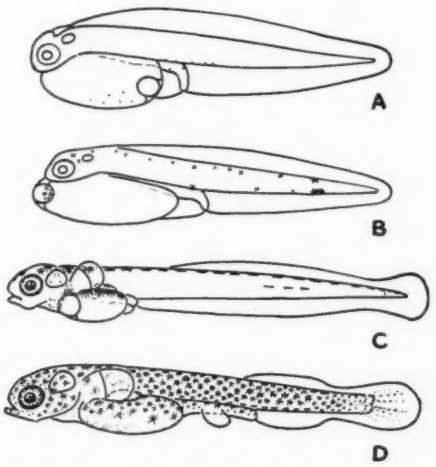


FIG. 5. Differences in morphological characters, pigmentation, and yolk reserves in the newly hatched larvae of some California marine fishes. *A*, Opaleye, *Girella nigricans*, Girellidae; *B*, Señorita, *Oxyjulis californica*, Labridae; *C*, Grunion, *Leuresthes tenuis*, Atherinidae; *D*, California flyingfish, *Cypselurus californicus*, Exocoetidae.

sorption development is carried forward to the juvenile stage. This specialized type of larva is commonly termed an alevin. Many teleosts, of widely divergent relationships, are live-bearing, and their developmental patterns show very useful taxonomic characters. For example, the structure of the trophotaeniae (nutritive rectal processes of the embryo) is now used as a major basis for the classification of the cyprinodont family Goodeidae (Turner, 1937; Hubbs and Turner, 1939), displacing tooth structure, which is subject to much convergence and had led to an erroneous classification.

Larval Characters As Indicators of Relationship

Basic anatomical characteristics that are shared by larva and adult (e.g., number of vertebrae) can be expected to follow closely co-ordinated evolutionary trends, for in general a major change in this type of character registers in both stages. But characters that are expressed in only one stage (e.g., horny beaks of tadpoles) may undergo evolutionary modifications that appear only in that stage. In such characters, larva and adult may undergo extensive independent evolution. Larvae can be expected to combine stable characters that vary in close accordance with the main categories of adult classification, with more plastic characters that undergo independent secondary modifications. The secondary trends may be so conspicuous and complex as to mask the more fundamental changes.

Frog tadpoles are notoriously difficult to identify. Their characters are highly specialized, and the seemingly unlimited variation shows little organization on preliminary study. The information now available, however, indicates that the variations and specializations fall into a simple evolutionary pattern of the kind revealed by a study of the adult stages of almost any group of animals, and explainable by the same principles.

Although many of the conspicuous larval characters are excessively variable, others are remarkably uniform throughout large taxonomic groups, regardless of how specialized the tadpole may be in gross appearance and in habits. On the basis of very conservative features of both internal and external anatomy, all of the nearly 600 kinds of tadpoles known to me either from original study or from published data can be grouped into four stable types (Fig. 6), each restricted to a family or a group of families (Orton, ms.). Some of the characters are briefly summarized here. Three of the types characterize the more primitive groups of families (as based on adult characters), which contain relatively few species. The fourth and most specialized larval type is numerically dominant, for it characterizes all of the more modern, and generally larger, families.

The first type characterizes the Pipidae and Rhinophrynidae, and is considered the most primitive, for it is the simplest and most nearly resembles larvae of other vertebrates. The spiracle (an opercular structure, not the hyoidean spiracle of fishes) is paired, and the right and left gill chambers are entirely separate. The mouth is a simple slit with narrow labial folds. The internal anatomy of the jaw region is relatively simple; notably, Meckel's cartilage is long and supports the entire lower jaw. The second and third types of tadpoles have a single midventral spiracle, draining both gill chambers. The second type characterizes the Microhylidae, a family of specialized frogs of uncertain relationships. Their larval characters, though not yet adequately understood, suggest that the family diverged at a much more primitive level than is commonly thought. The mouthparts of microhylids are more complex than in the pipid type, but are still comparatively simple. The basic characters of the mouthparts are constant in all microhylids so far as known, though these larvae vary somewhat in feeding habits and include at least one carnivorous form. The third larval type, characterizing the Discoglossi-

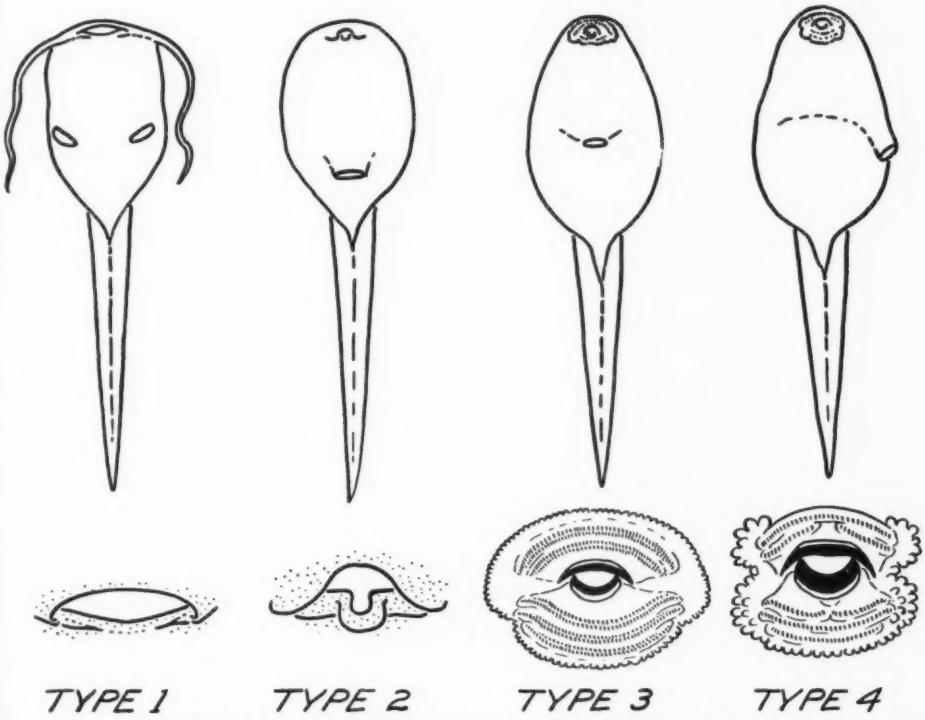


FIG. 6. Ventral views and mouthparts of basic types of tadpoles, to show external characters of each. Generalized diagrams.

dae and Ascaphidae, has elaborate mouthparts, including wide lips, horny beaks, and labial teeth in transverse rows, all or most of which develop more than one line of teeth per tooth ridge. The jaw cartilages and their musculature are complexly differentiated. In the fourth type the spiracle is single and asymmetrical, on the left side, and drains both gill chambers. The highly differentiated mouthparts are similar to the third type, but differ in having the labial teeth in single rows (with rare exceptions); certain internal characters also differ.

Because of the well-recognized need for caution against relying too heavily on "nutritional" characters in classification, emphasis has been accorded study of the internal anatomy of larvae that are highly modified for unusual habits or ecological situations. The many variations and peculiar specializations found thus far in such larvae all fall within the framework of the basic types.

Each of the basic types probably represents the condition of the larval stage at a major level of evolution. Neither the larval types nor the groups of adult frogs can be arranged in a linear phylogenetic sequence. Evolution has unquestionably been elaborately radiative in the frogs, as in other animals, and important evolutionary stages have certainly been lost by extinction during the long history of the group.

Within each of the four basic larval types there are well-defined secondary trends that illustrate adaptive radiation and convergence just as clearly as these principles are shown in adult stages.

In patterns of adaptive radiation, the larvae of a taxonomic unit share certain major characters, but in other respects they show divergent modifications that adapt them to different ecological conditions or different ways of life (Fig. 7). No matter how diverse in superficial appearance, however, they retain basic characters indicative of their relationship. The adaptive types include deep-bodied, high-finned nektonic larvae; mountain-stream larvae with an enlarged, flattened snout, huge vacuum-cup mouthparts, and heavy axial musculature; carnivorous forms with hypertrophied beaks and jaw muscles; thin, flattened larvae that live in bromeliads and other restricted arboreal aquatic niches; forms with mouthparts upturned for surface-feeding; and specialized embryos with direct development. There is evidence that adaptive radiation has occurred repeatedly in tadpoles. It is shown at the level of each of the four basic types, within most of the families, and within some of the larger and better-known genera (notably *Hyla* and *Rana*).

In convergent evolution, larvae of different taxonomic groups secondarily and independently develop a common adaptive type. Although they may be strikingly similar in superficial respects, they retain the basic characters that reveal their diverse origins. Convergent evolution is conspicuously shown in several larval modifications. For example, mountain-brook larvae that look much alike (Fig. 8) have evolved independently in at least six of the approximately thirteen families of frogs. Surface-feeding larvae of strikingly similar appearance (Fig. 9) are known in four families. There are examples of direct development in nearly all families.

Larval fishes also show abundant evidence of variability, species differences, and group resemblances. Modifications in larval and other developmental characteristics have unquestionably followed standard patterns of evolution in fishes, as in

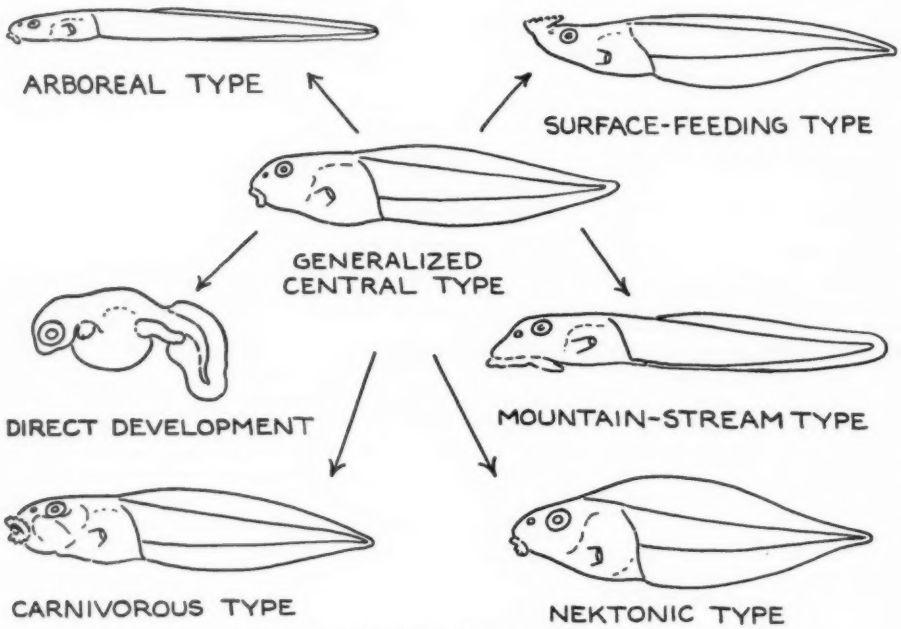


FIG. 7. Adaptive radiation in tadpoles.

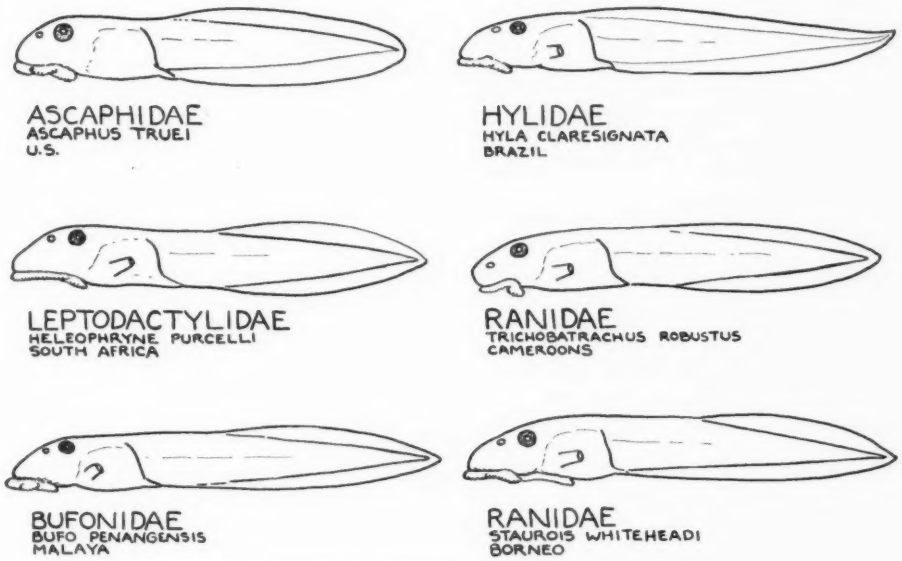


FIG. 8. Convergent evolution in tadpoles of swift streams.

the frogs. The problem of working out and interpreting these developmental characters and trends is one of the frontier areas of systematic ichthyology.

Origin of New Larval Types

The highly complex nature of the frog tadpole, in contrast to other known types of amphibian larvae, presents a problem in larval systematics at the ordinal level. The few known larvae of extinct groups of amphibians were very generalized. In fundamental form, though of course not in details, they closely resembled the larvae of present-day salamanders. The jaws were long, with simple functional arrangement, the body was relatively long, and the limbs and girdles were of simple proportions. Some fossils show evidence of external gills. The earliest amphibians and the primitive crossopterygian stock from which they arose probably shared this very generalized larval type (or something essentially similar to it), with a minimum of special larval structures and a simple metamorphosis. The very long persistence of the simple larva suggests that it has great stability. The present-day lungfishes and salamanders still retain the essential features of this primitive larval type, though they are only remotely and indirectly related to each other.

The frog tadpole contrasts sharply with the primitive larva in having a unique combination of distinctive characters. It has a short compact head-body unit, supported by a very short vertebral column, and sharply demarcated from the long tail. The gills and front leg buds are concealed under a closed operculum that retains one or two small excurrent openings. The mouth is small and usually has elaborate external parts; its internal parts are greatly modified and displaced far forward. The intestine is spirally coiled and is usually very long. The highly specialized plan of the frog tadpole is most commonly explained as an adaptation for vegetarian or scavenger habits, in contrast to the carnivorous habits of the adult. Carnivorous habits do, however, characterize

a few tadpoles, e.g., those of the *Rana rugulosa* group, but such larvae retain and even further specialize the elaborate characters of their taxonomic group. They show no simplification or basic changes of structural plan such as one might expect if complex mouthparts were directly correlated with adaptation to vegetarian habits. Larval anatomy suggests that vegetarian habits may be a subordinate character, and that a very different primary factor governs the larval type in the frogs. The larval and adult stages differ sharply in most respects, but they do share some of the specializations that place the Salientia well apart from all other known amphibians. Above all, both tadpole and frog have the vertebrae excessively reduced in number (only 6 to 9 presacrals) without a compensating increase in the length of the individual elements. The shortening of the vertebral column is so fundamental that the change almost certainly evolved simultaneously in both stages.

Larva and adult have compensated for reduction in the length of the vertebral column by very different anatomical adjustments (Fig. 10). In the frog the presacral vertebrae occupy only about half the length of the trunk. The minimum space necessary for the viscera has been retained by extending the body cavity backward beyond the sacral region. This posterior extension is supported by three bones: the two greatly elongated, horizontal ilia, and the median urostyle, a caudal element transferred into the body. The enlarged hind legs and jumping habits of the frog are commonly considered primary characters, but it is more likely that they evolved as secondary concomitants of the trend toward excessive shortening of the vertebral column, with its decreased body flexibility and loss of the tail as a locomotor or balancing organ. Space adjustments in the tadpole have been accomplished by excessive displacement and crowding of structures, especially by the forward shift and reorganization of the jaws and gill-arch system, and by displacement of the forelegs and their concealment with the gills under the modified operculum. The gill-raker system is usually large and elaborate. Its actual use as a filter-feeding device in many tadpoles, especially pipids and microhylids, suggests

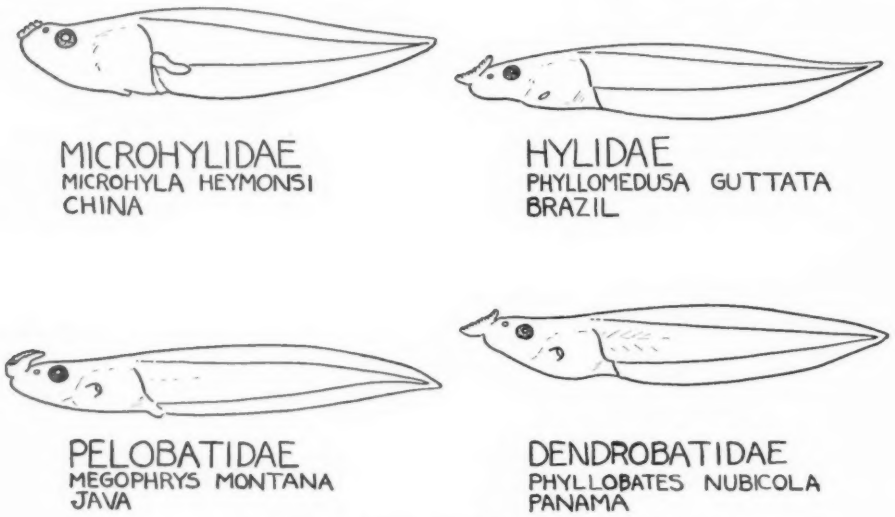


FIG. 9. Convergent evolution in surface-feeding tadpoles.

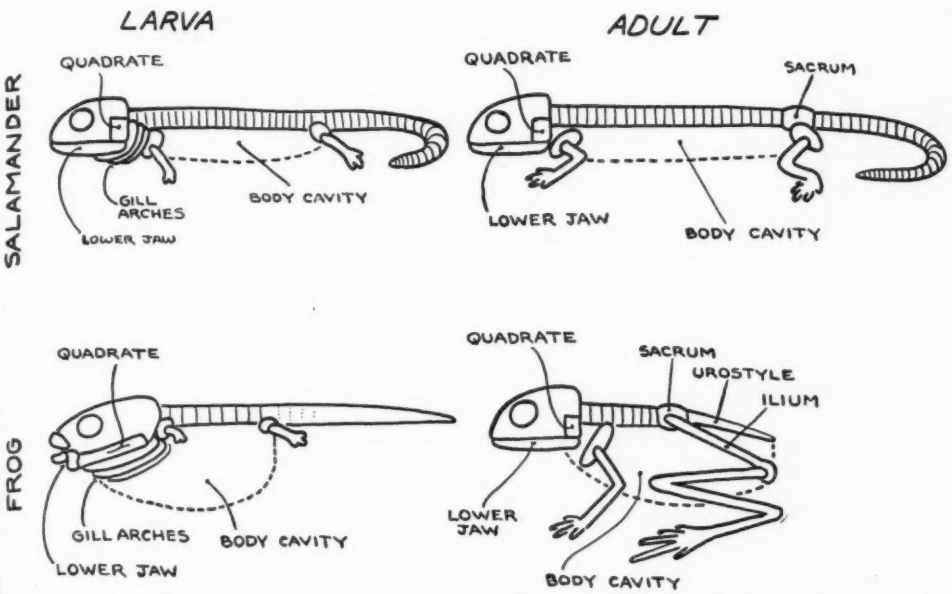


FIG. 10. Diagrams to illustrate theory that displacement of structures in frog tadpole, and skeletal peculiarities of adult frog, are correlated primarily with phyletic shortening of vertebral column.

that the transitional larval types were probably plankton-feeders. The more modern of the extant types have hard beaks and grasping labial teeth, and are most commonly herbivorous or feed primarily by chewing on miscellaneous organic material. The enlargement of the digestive tract to accommodate vegetarian habits has led to still further crowding of the shortened body cavity.

The known fossil record is of little direct assistance in tracing the origin and evolution of the frog tadpole. But the theory that the shortening of the vertebral column was the basic factor in the origin of this type of larva can account for all of its chief distinguishing features, and the theory correlates major events in both larval and adult evolution. Larval and transitional stages of the Triassic *Protobatrachus* could provide critical evidence bearing on the problem, but this very primitive pre-frog is still known from a single adult specimen.

A trend toward excessive shortening of the vertebral column could lead to rapid extinction if the group lacked sufficient genetic adaptability to permit the evolution of compensating trends. In the frogs, the larval and adult stages, as a co-ordinated unit, succeeded in establishing a very distinctive new anatomical plan, a starting point for an evolutionary radiation that is unusually rich in new taxonomic characters. Although the frogs are now a very old group, the wide distribution and great diversity of specialized types that they still maintain (in both larval and adult stages) mark them as a highly successful evolutionary "accident."

Larval stages may have had an important role in the early history of still higher categories. Several authors, including Garstang, de Beer, Romer, and Gregory, have contributed in various ways to the theory that the entire phylum Chordata may have been established by neoteny from some stock in which the larva

was the active stage and possessed the notochord and somites as larval specializations for the support and function of the tail. The adult stage was perhaps sluggish or even sessile. The branchial basket probably functioned originally (in both stages) as a food-filtering apparatus and only later became remodeled for respiratory purposes, after the function of food-snatching had been taken over by jaws.

Summary

A study of the larval stages of fishes and amphibians reveals much important data on their systematics and evolution. Standard methods and theories of modern systematic zoology can be applied directly to the interpretation of larval characteristics. Both larvae and adults show variability, species differences, and group resemblances. In both stages, one can demonstrate primary trends indicating major relationships and secondary trends involving adaptive radiation, convergence, and other evolutionary phenomena. Basic characters of anatomy that are shared by larva and adult (e.g., number of vertebrae) can be expected to follow closely co-ordinated evolutionary trends, for in general a major change in this type of character registers in both stages. But characters that are expressed in only one stage (e.g., horny beaks of tadpoles) undergo evolutionary modifications that appear only in that stage, and in such characters larva and adult can undergo extensive independent evolution. Larvae can be expected to combine conservative characters that vary in close accord with the main categories of adult classification, with more plastic characters that undergo independent secondary modifications. The secondary trends may be so conspicuous and complex as to mask the more fundamental changes.

These general principles are illustrated particularly well in the tadpole stage of the frogs. Indeed, the picture is so clear-cut in this group that it provides an excellent small-scale working model for the study of the vastly more complex larval problems of the fishes. On the basis of very conservative features of both internal and external anatomy, known tadpoles fall into four types, each restricted to a family or a group of families. Each of these basic types probably represents the condition of the larval stage at a major level of evolution. Within each type there are well-defined secondary trends, especially of adaptive radiation and convergent evolution. There is evidence that these trends have evolved repeatedly in tadpoles. They are shown not only at the level of each of the four basic types, but also within most families and within some of the larger and better-known genera. Other specialized life-history patterns, such as neoteny and secondary direct development, have also evolved independently in unrelated stocks.

The highly complex frog tadpole contrasts sharply with other known types of amphibian larvae and with larval fishes, and its interpretation is a major problem in larval systematics. It is suggested that the peculiar combination of characters of the frog tadpole originated as an adjustment to acute internal space limitations resulting from the extreme shortening of the vertebral column. The origin of the tadpole type of larva is thus considered to be an integral phase of the origin of the order Salientia.

Larval stages may have had an important role in the early history of still higher categories. It is now rather widely thought that the entire phylum Chordata may have originated by neoteny from some stock in which the notochord and somites had been larval characters.

REFERENCES

DE BEER, G. R. 1951. Embryos and ancestors (revised ed.). Oxford Univ. Press.

GREGORY, W. K. 1946. The roles of motile larvae and fixed adults in the origin of the vertebrates. *Quart. Rev. Biol., 21,* 348–364.

HUBBS, C. L., and TURNER, C. L. 1939. Studies of the fishes of the order Cyprinodontes. XVI. A revision of the Goodeidae. *Misc. Publ. Mus. Zool. Univ. Mich.,* No. 42, pp. 1–80.

ROMER, A. S. 1946. The early evolution of fishes. *Quart. Rev. Biol., 21,* 33–69.

TURNER, C. L. 1937. The trophotaeniae of the Goodeidae, a family of viviparous cyprinodont fishes. *J. Morphol., 61,* 495–523.

This is the second of three papers which comprised the Symposium on "Life History Studies in Relation to Systematics," sponsored by the Society of Systematic Zoology and the AAAS, St. Louis, December 27, 1952. **GRACE L. ORTON** is a member of the staff of the Scripps Institution of Oceanography, University of California, La Jolla. The material on tadpoles is based largely on the author's Ph.D. thesis, University of Michigan. Contribution from the Scripps Institution of Oceanography, New Series, No. 633.

ANNOUNCING—a NEW journal:

THE ITINERANT NATURALIST

A journal devoted to obscure animals, obscurely published.

To be published every three months by hand on a Washington press, in 18 pt. Caslon Oldstyle; page size, 15×24 inches. Illustrations will consist of woodcuts, to be submitted in a finished condition by the authors.

Papers should be submitted in legible Spencerian hand (using Higgins Eternal Ink)* on ruled foolscap, not less than 50 words and not more than 2,000 words in length, on the systematics, bionomics and unseasonal occurrence of organisms found under stones, in moist logs, moss beds, or similar biotopes, terrestrial, fresh water or marine. Descriptions of new species and notes on sexual behavior will be given priority.

Illustrations must not be larger than 2×3 cubits; graphs, when necessary, must not be more than one inch square.

Papers will be critically read and altered by a board of editors; proofs will not be furnished.

THE ITINERANT NATURALIST will be distributed gratis only to star route county branch libraries and remote, transmontane junior colleges.

Table of contents for Vol. I., no. 1:

Some ecological notes on a Triassic trilobite. —J. Willoughby Fortescue

A new genus (and new family) of stamenophilous mollusks from Equisetum. —Q. Johannes Betulaceae

Crepuscular periodicities in sexual vigor in an arboreal flatworm (gen. et. sp. nov.). —Hieronymous Wombat, F.L.S., F.R.S.

An unusual occurrence of Jones side-hill salmon in Deer Creek, with 15 new subspecies. —Anonymous

Subscribe now, to ensure an unbroken set of this important new periodical.

Subscription rates: $15 per annum, payable in advance to Joel W. Hedgpeth, Scripps Institution of Oceanography, Univ. of California, La Jolla.

* Genuine cuttlefish sepia also acceptable.

NOTE: As we do not have any italic type, italicised matter will be set in a short font of worn 6 pt. German textletter.

An Application of Factor Analysis to the Systematics of *Kalotermes*

CLYDE P. STROUD

MULTIPLE factor analysis, as developed chiefly by Thurstone (1931, 1945*a*), is a general method which can be adapted to a wide variety of problems. Like other forms of multivariate analysis it constitutes a method for the examination of complex sets of phenomena, expressed either in terms of experimental or nonexperimental data, in an attempt to account for most of the variance of the observed values in terms of a restricted number of underlying parameters, factors, or explanatory concepts. It is particularly useful as an exploratory method for the investigation of certain kinds of complex domains, especially where one or more of the following conditions prevails: (1) the underlying causes are unknown; (2) the underlying causes cannot be controlled; (3) the underlying causes are very numerous; (4) the basic question of the investigation tacitly forbids any alteration of the underlying causes.

This method stands in an intermediate position between two extremes of multivariate analysis. On the one hand the object of analysis may be maximum parsimony of description in terms of wholly arbitrary parameters, such as the principal axis method as developed by Hotelling and others. At the other extreme is the method of path coefficients as developed by Wright (1918, 1921, 1923, 1932, 1934), which permits a great deal of freedom in the introduction of hypotheses based on knowledge additional to that included in the table of correlations of the variables.

Multiple factor analysis differs from purely statistical methods in that it does not always involve the same set of assumptions as do the usual statistical models, and in that there have not been developed, as yet, adequate methods of establishing degree of confidence in the findings obtained. Discoveries made by multiple factor analysis could be related to statements of reliability in either of two ways. In some cases findings could be subjected after discovery to more refined statistical techniques which can establish reliabilities. It is also possible that in many applications, assumptions basic to statistics could be made at the outset and appropriate sampling error criteria applied. It is hoped that a further relation of multiple factor analysis to statistics can be developed.

In favor of multiple factor analysis it must be said that it is a comparatively easy method of obtaining exploratory information of a semireliable nature about many kinds of complex phenomena. The addition of techniques to establish statements of reliability would doubtless greatly increase the work involved in an analysis. Whether they are to be applied directly with the factor analysis, applied afterwards to verify the results of the analysis, or not applied at all, is a judgement to be made in terms of the nature of the problem at hand. A characteristic of multiple factor analysis which makes it particularly useful for certain types of studies and less useful for other types is that it employs a standard set of simple assumptions in all applications, and derives its findings from the coefficients of correlation alone. Only in the interpretation of the findings are data extraneous to the correlations introduced.

Some facets of the central problem of systematic biology—which may be defined as the relation of organisms to each other—lend themselves remarkably well to

investigation using a method such as multiple factor analysis. Four kinds of information are developed relative to this problem: (1) organisms are assigned to categories corresponding as closely as possible to their phylogenetic relationships; (2) characters are evaluated with regard to their relations to each other and their reliabilities as indices of closeness of kin; (3) phylogenies or historical lines of descent are discovered and related to the categories and characters of organisms; (4) the evolutionary processes are studied in relation to characters which define categories and to phylogenies which generate categories. Multiple factor analysis can make substantial contributions to the organization and integration of all these four related kinds of information.

Materials and Methods

The material studied in the present work consisted of specimens of more than fifty species of termites belonging to the genus *Kalotermes*. This is the most primitive living genus of the family Kalotermitidae, which contains eight other genera. The kalotermitids are a primitive family of termites remotely related to the more primitive family Mastotermitidae, represented today only by a single Australian species (Ahmad, 1950). The chief criterion of primitiveness here is the possession of blattoid characteristics, since the evidence for the descent of the termites from primitive cockroaches is very clear and probably irrefutable.

In addition to the possession of blattoid characteristics, the genus *Kalotermes* shows its primitive aspects in other ways. It is a group in which many species show such a wide range of individual variation that specific characters are often difficult to ascertain reliably. Characters involving serially replicated components are highly variable. The number of such elements is usually relatively large and variable, and they show relatively little differential specialization among themselves.

Measurements were made on soldiers (usually a single specimen) of each of 48 species of this genus, and on imagoes of 43 species. Because of the time consumed in making accurate measurements and in dealing with the additional analytical problems involved, the element of individual variation within a species was not studied by measurements of a large number of individuals of those species for which they were available. However, for two species, *K. snyderi* and *K. immigrans*, two soldier specimens of each species were measured, and the results give some hint of the relationship of individual variation to the study. Variation within the species should be investigated by a combination of the techniques of analysis of variance and of covariance with the factor analytical methods of the present study.

Each specimen was measured for an array of fourteen characters. The choice of characters was made in such a way that homologous dimensions of soldier and imago anatomy were measured. The measurements were scattered over the body as much as possible, rather than being concentrated in a particular region. Characters were also chosen in such a way that measurements were made on hard, sclerotized regions of the body, thereby minimizing errors due to handling or positioning of the specimens. The characters so selected are listed below:

1. Length of right mandible.
2. Length of second antennal segment.
3. Length of third antennal segment.
4. Length of third (metathoracic) tibia.
5. Width of third tibia.
6. Width of third femur.
7. Height of head.
8. Length of head.
9. Width of head.
10. Length of pronotum.
11. Width of pronotum.
12. Length of postmentum.
13. Width of postmentum.
14. Maximum diameter of eye.

The method of multiple factor analysis was introduced by Thurstone (1931). Previous to this, a number of other

workers employed various types of multivariate analysis to data of different kinds. Since 1931 multiple factor analysis and related methods have been employed very extensively in psychology by Thurstone (1945*a*), Holzinger and Harman (1941), Kelley (1935), Thomson (1939), Burt (1941), and others. The methods have been applied to anthropometry by Burt (1938), Cohen (1938, 1939–1941), Hammond (1942), McCloy (1940), Moore and Hsu (1946), Rees and Eysenck (1945), and Thurstone (1945*b*, 1946).

It was expected that information of some interest might be gained by studying the measured characters of *Kalotermes* by factor analysis. Such a study might permit an evaluation of the characters as to their usefulness in describing subgroups within the genus, and might also make it possible to relate characters to evolutionary trends for the genus as a whole. Moreover, the results could serve as the basis for a comparison with some more specialized genus.

It was found that all the measured characters were distributed approximately normally both in the soldier caste and in the imago caste over the population of species measured. Most of the characters show some skewness, always in the same sense. There are a relatively small number of species having quite large values and a large number of species having moderately small values. Bimodality is suggested for some of the characters but is not demonstrable at a significant level with the relatively small number of measurements made.

Factor analysis makes the assumption of the additive combination of factors, whereas such factors as those of the present study may often combine more nearly as multiplying factors in the sense used by Wright (1921). As Wright pointed out, the error term in considering additive combination as an approximation of multiplicative combination is small unless the amount of variation in the causative factors is large in comparison with the mean values. The additive assumption of factor analysis is that for the uncorrelated common factors a,

$$s_{ij} = \Sigma_a x_{ia} u_{aj} + \delta$$

where δ is due to unique factor and error variance.

The skewness of the data suggests that a change to logarithmic scale might have improved the study, but it was thought best to abstain from the additional complication in this, the first factor analytical approach to a systematic problem.

Product-moment coefficients of correlation were computed relating each character to each other character. This was done separately for the imago and soldier caste studies.

It is assumed that the regression of one variable on another, if not linear, is at least monotonic so that the use of linear coefficients of correlation is approximately correct. Whether or not the factors have a Gaussian distribution over the population studied need not concern us at present (Thurstone 1945*a*, pp. 63–67). It would be interesting to compare the results of the analysis of these coefficients of correlation with those obtained on the logarithms of the measurements.

Each of these correlation matrices R was then factored by the complete centroid method (Thurstone 1945*a*, pp. 149–157). In this method the correlations are accounted for in terms of a number of parameters much smaller than the number of measurements. The projections of the character vectors on the axes of the "common factor space" are given as a matrix F whose rows represent the measurements and whose columns refer to the orthogonal factor axes. These projections are called the centroid factor loadings.

The length of a character vector is the square root of the corresponding "communality," h_j^2, or the proportion of the whole variance of the measurement which enters into the correlations.

Thus, the correlation between a pair of characters j and k,

$$r_{jk} = \sum_{a=1}^{b} f_{ja} f_{ka} + \epsilon$$

where the subscripts a refer to the orthogonal factors. The quantity ε is a residual which is vanishingly small.

The communality,

$$h_j^2 = \sum_{a=1}^{b} f_{ja}^2$$

In matrix notation

$$F \cdot F' \doteq R$$

a matrix whose non-diagonal entries are, approximately, the coefficients of correlation. The entries in the principal diagonal of R are the communalities.

Since the communalities were unknown at the outset of the study, these were estimated for a first factoring (Thurstone 1945*a*, pp. 299–300), then corrected for a second factoring. Those obtained from the second factoring did not differ substantially from the estimates based on the first factoring, so that further iteration of the factoring process was not necessary.

The coefficients of correlation and the communalities are so related to the angle ϕ_{jk} between pairs of character vectors that

$$r_{jk} = h_j h_k \cos \phi_{jk}$$

The position of the first centroid axis is located in such a way that it passes from the origin through the centroid of the termini of the measurement vectors. It thus lies approximately in the longest axis of the hyper-ellipsoidal region occupied by the measurement vectors. In cases such as these, where all the correlations are positive, this is strictly true and all the measurements have positive projections for this first centroid axis, as all the measurement vectors lie in the same half of the hyper-ellipsoid.

The "residual correlations"

$$r_{(-1)jk} = r_{jk} - f_{j1} f_{k1}$$

are computed, and the table of these is then analyzed to obtain positions for the second centroid axis. Strictly speaking, this second axis (and this is true of subsequent axes as well) does not pass through the centroid of the residual vectors. This centroid is near the origin since the sum of the residual correlations is near zero. Instead, the second axis passes from the origin through the centroid of a system of termini of vectors, some of which have been "reflected" so that all lie in the same half of the residual hyper-ellipsoidal space. It does not really matter much where the second axis is placed so long as it is orthogonal to the first and accounts for a large amount of the variance involved in the residual correlations. Arbitrarily, vectors are reflected one at a time starting with that vector the sum of the residual correlations of which has the greatest negative value, and continuing until no sum of the residual correlations of a vector, corrected for the vectors reflected, is negative. The projections of the original vectors on this axis are determined and a second set of residual correlations $r_{(-11)jk}$ are computed.

The process is continued until all entries $r_{(-b)jk}$ are vanishingly small. These are the "residuals" and are to be ascribed, largely, to errors of estimate of the correlations.

The first centroid axis may have some biological significance but the others are certainly no more than convenient arbitrary orthogonal axes for the description of the vectors in the common factor space. This space is of b dimensions, where b, the number of factors, is considerably less than the number of characters. It is important to devise a statistical means of determining the best value of b.

Many factor studies have been carried only to this point. In other cases the axes have been located by least-squares fitting instead of the simple centroid method. It was obviously desirable to try to find a simple hypothesis about the relation of factors to characters so that meaningful interpretations of factors could be made.

One such hypothesis is furnished by Thurstone's simple-structure concept. The hypothesis is that for any meaningful common factor (other than a general factor) one would expect to find a subset of the original characters on which the factor has no (or only a very small) influence. The vectors representing such characters would lie in (or very nearly in) a subspace of $(b-1)$ dimensions of the b-di-

mensional common factor space. The factor axis could be described as orthogonal to this null subspace. Similarly a whole class of b or more or less factors might be located in this way with the axis of each orthogonal to a $(b-1)$-dimensional subspace containing the vectors on which a given factor does not act.

A brief set-theoretical interpretation of the simple-structure concept seems helpful. Denoting by B_p the set of vectors on which factor P has no influence, a complete simple structure can be said to exist if there is a set B_p for each of the b factors P, and if

$$\begin{array}{r} B_1 \neq B_2, B_1 \neq B_3, \ldots B_1 \neq B_b \\ B_2 \neq B_3, \ldots B_2 \neq B_b \\ \ldots \qquad \ldots \\ B_{b-1} \neq B_b \end{array}$$

that is, all intersections of pairs of sets contain fewer elements than the corresponding unions,

$$(B_p \cup B_q) - (B_p \cap B_q) \neq O$$

Thus in a given study a particular subset of the variables can determine one and only one group factor. If there are two (or more) group factors having the same null subset of variables, their presence can only be determined by additional studies in which supplementary variables are introduced so that this is no longer the case. The relativity of the unitary nature of factors is not necessarily unfortunate, especially in applications to domains in which the number of ultimate factors is legion and what are really sought are major groups of ultimate factors. Of course there is no point in reporting as separate, two group factors P and Q, whose null subsets B_p and B_q are really a pair of approximations to what is actually the same null subspace. In a case such as this, either $r_{pq} \doteq 1$ or $r_{pq} \doteq -1$.

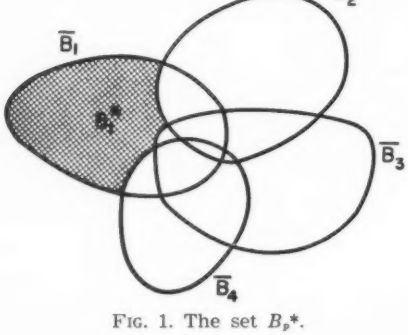


FIG. 1. The set B_p^*.

A quantitative test could be based on determining the rank of the matrix R_{pq}, the entries of which are the correlations of the primary factors (with unity as the entries of the principal diagonal), and seeing that this is equal to its order. For studies with high communalities (which are common in morphological as opposed to psychological studies) the coefficients of correlation of the variables have smaller standard errors so that primary group factors which are relatively highly correlated with each other can be discerned.

The complement of B_p, denoted $\overline{B_p}$, is the set of characters which can be used to describe the factor P, as these are the measurements on which factor P exerts an influence. A set B_p^*, which may be defined by a relation such as

$$B_p^* = \overline{B}_p - \overline{B}_p \cap (\overline{B}_1 \cup \overline{B}_2 \cup \ldots \cup \overline{B}_{p-1} \cup \overline{B}_{p+1} \cup \ldots \cup \overline{B}_b)$$

contains only characters which are influenced by no group factors other than P. The set B_1^* is indicated as the shaded portion of set $\overline{B}_1$ in Figure 1 for a case in which $b = 4$. Obviously, the elements of B_p^* describe the action of factor P in its purest form. In Figure 2, the projections of the termini of vectors are shown on a two-dimensional subspace including the origin O of the system. The two axes represent the factor axes P and Q and lie in this plane. The points representing the termini of character vectors can be assigned to sets $\overline{B}_q$, B_q, $\overline{B}_p$, and B_p.

The rotational process is one in which a search is made for a set of $\frac{b(b-1)}{2}$ such planes (for the case where all b common factors are group factors), each containing a pair of factor axes, by locating the "streaks" of projection points which de-

fine the null subspaces of factors as they appear in the two-dimensional projections of the space. These factors need no longer be orthogonal to each other. A rotational matrix Λ is found. Then

$$F \cdot \Lambda = V$$

where V is a new matrix in which the number of zero (or near zero) entries is maximized. When the columns of V are plotted against each other, a set of diagrams similar in general form to Figure 2 is obtained. These are characterized by the fact that a good number of the points lie on or near the lines representing zero values for the factors. The rotated factor matrix V is examined, and each factor is interpreted in terms of the characters for which it has high loadings.

It was of interest to compute approximate factor evaluations for the individuals measured in the study. The method used is based on the discussion by Thurstone (1945*a*, pp. 511–516), and elsewhere. First, the matrices S_{ij} of the standard values for each individual i for each measurement j were computed. Next, the reciprocal or inverse matrix R_{jk}^{-1} of each correlation matrix (with unit diagonal entries) was obtained. The method as given by Thurstone (1945*a*, pp. 46–48) after Tucker (1938) was satisfactory except that it was necessary to carry all numbers to four decimal places in order to have satisfactory accuracy as the rounding errors accumulate in the process. For each caste a matrix T_{ap} is needed to relate the rotated factors to the centroid axes. It is obtained by

$$T_{ap} = (D \cdot \Lambda^{-1})' = (\Lambda^{-1})' \cdot D$$

where D is a diagonal matrix, each of whose entries is the reciprocal of the square root of the corresponding entry in the principal diagonal of the matrix

$$M = C^{-1} = (\Lambda' \cdot \Lambda)^{-1}$$

It should be noted that C is the matrix of the cosines c_{pq} of the angles θ_{pq} between pairs of primary factor axes P and Q. Furthermore the matrix of the correlations of the primary factors

$$R_{pq} = D \cdot M \cdot D = D \cdot C^{-1} \cdot D$$

Then

$$W_{ja} = R_{jk}^{-1} \cdot F_{ka}$$

and

$$W_{jp} = W_{ja} \cdot T_{ap}$$

are matrices whose entries are the regression weights for the characters on the centroids and on the rotated factors respectively.

Finally these weights were applied to the standard values:

$$S_{ij} \cdot W_{ja} = X_{ia}$$
$$S_{ij} \cdot W_{jp} = X_{ip}$$

to obtain matrices X which are evaluations of the individuals i for the centroids a and the rotated factors p respectively. The evaluations x_{ia} and x_{ip} are subject to errors due to values δ attributed to unique factors and error variance as shown in the fundamental additive equation. The matrix W_{ja}, which relates S_{ij} to X_{ia}, the evaluations for the centroids, is simply related to the matrix U_{aj} of values u_{aj} of the fundamental additive aquation by:

$$W_{ja} = U_{aj}^{-1}$$

where the squares of the residuals δ due to unique factors and error variance have been minimized. Matrix X_{ia} gives the coordinates of points representing the measured individuals in a space of b dimensions, represented by the orthogonal axes a.

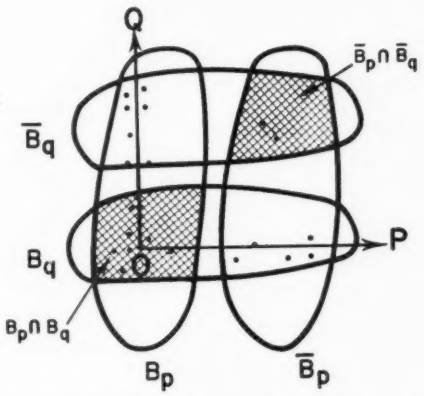


FIG. 2. Projections of termini of vectors on plane containing a pair of group-factor axes.

In addition to other sources of error, a species, which should be represented by a cluster of points, each determined by the evaluations for a single individual, is represented in this study by the evaluations of a single individual. There are two exceptions to this in the soldier caste. The relation of this individual variation to Centroid I (size) and to primitiveness should be studied further.

The matrix X_{ia} is a convenient starting point for an examination of the points to see if subsets corresponding to systematic categories can be discerned. The underlying assumption is that a group of species, all descended from a single branch of an early dichotomy, and represented by a single interbreeding population for some time before further dichotomy, would be expected to differ from other members of the genus by some combination of attributes. That combination of attributes for which the variance of the group is minimized is found by rotation. The points representing members of the group then lie approximately in a subspace of $(b-1)$ dimensions. It should be noted that only large subgroups can be found by this means. A subspace of $(b-1)$ dimensions can be fitted exactly to any set of b species; hence only groups containing considerably more than b species can be demonstrated.

The search for such groupings was made in a manner analogous to the single plane method of rotation (Thurstone, 1945*a*, pp. 216–224). Some species S_1 is chosen as the starting point in the search for each species-group. It is assumed that this species is to be a member of the group to be located. A first trial axis, α_1, is located, running from the origin through the point representing the species chosen. The direction cosines $\lambda_{a_1 a}$ of this axis are obtained by normalizing the set of centroid evaluations $x_{s_1 a}$ of species S_1.

The entire set of species is then evaluated for projections on this axis α_1, and the resulting values are plotted as the ordinate, using each centroid axis in turn as the abscissa. These diagrams are then examined for subspaces of $(b-1)$ dimensions near S_1 as indicated by streaks of points including S_1. A line is drawn through S_1 in the direction of each streak. A parallel to this line is drawn from the origin to the intersection with the ordinate at the unity centroid value. The value of the ordinate of intersection is entered as s_{aa} in the equation

$$\Psi_{a_2 a} = \frac{\lambda_{a_1 a} - s_{aa}}{1 - s_{aa} \lambda_{a_1 a}}$$

The obtained values of $\Psi_{a_2 a}$ are then normalized by

$$\lambda_{a_2 a} = \frac{\Psi_{a_2 a}}{\sqrt{\sum_a \Psi^2_{a_2 a}}}$$

to obtain the direction cosines of a second approximation to the axis, α_2. The process is continued until a streak including S_1 is demonstrated or is shown not to exist.

Results

Table I lists the coefficients of correlation of pairs of characters in the imago caste and in the soldier caste respectively. The highest correlation for a pair of characters of the soldier caste is nearly 0.98 between head width and pronotum width. It is found that this especially high correlation is interpretable in terms of the factor analysis and is of great adaptive significance. Other very high correlations are found between the length of the tibia and the length of the pronotum and between the height and width of the head. Both these are also related to adaptive trends found by the factor analysis. The lowest correlations for the soldier caste are those between tibia width and the two antennal segment measurements, and the correlations of postmentum length with third antennal segment length and with eye diameter. All but the lowest two correlations are significant at the $p < .01$ level, and one of these is significantly different from zero at the $p < .05$ level.

For the imago caste none of the correlations is as high as the two greatest soldier correlations. The highest are the correlations relating the two measurements

TABLE I—COEFFICIENTS OF CORRELATION

SOLDIER CASTE—MATRIX R_{jj}—ABOVE PRINCIPAL DIAGONAL

	1	2	3	4	5	6	7	8	9	10	11	12	13	14
1	—	.685	.663	.857	.679	.741	.867	.802	.877	.865	.862	.682	.889	.657
2	.588	—	.761	.571	.350	.488	.560	.490	.535	.586	.537	.446	.548	.413
3	.455	.451	—	.528	.389	.598	.494	.446	.587	.539	.653	.231	.473	.572
4	.735	.655	.633	—	.788	.850	.815	.813	.823	.927	.827	.801	.892	.597
5	.809	.487	.417	.756	—	.862	.760	.756	.790	.807	.800	.668	.811	.500
6	.760	.529	.438	.790	.897	—	.728	.768	.790	.866	.812	.668	.800	.501
7	.765	.648	.542	.821	.792	.828	—	.865	.939	.819	.910	.714	.888	.606
8	.761	.551	.584	.780	.878	.902	.858	—	.863	.840	.845	.844	.814	.528
9β	.820	.570	.595	.805	.904	.894	.910	.937	—	.864	.979	.647	.884	.694
10	.827	.589	.505	.838	.892	.905	.895	.884	.930	—	.895	.765	.886	.612
11	.820	.610	.572	.864	.861	.876	.880	.878	.919	.946	—	.636	.874	.666
12	.679	.611	.616	.774	.724	.717	.759	.754	.802	.757	.743	—	.780	.357
13	.644	.518	.415	.815	.769	.778	.802	.756	.833	.834	.846	.680	—	.579
14	.610	.488	.433	.817	.684	.740	.641	.709	.784	.738	.742	.578	.573	—

IMAGO CASTE—MATRIX R_{im}—BELOW PRINCIPAL DIAGONAL

of the pronotum, the correlations of head width with head length and height, and with pronotum length and width, and between the width of the femur and the lengths of head and pronotum. The relation of these high correlations to the factors is very complex in the imago caste.

None of the correlations of imago characters is as low as the lowest correlations of the soldier caste. All the imago correlations are significant at the $p<.01$ level. These facts suggest that adaptive evolution has acted in different ways on the two castes. In the imago caste a single general pattern of characters seems to be favored for all species, whereas in the soldier caste different combinations of characters are especially adapted to ecological differences of the species. Hence the correlations of the imago characters do not range as high or as low as those for soldiers.

Table II gives the centroid matrices of the soldier and imago castes. It should be noted that although five factors suffice to account for the soldier correlations, six are involved in the correlations of imago characters.

TABLE II—CENTROID MATRICES

	SOLDIER CASTE—F_{jj}					IMAGO CASTE—F_{im}					
	I	II	III	IV	V	I	II	III	IV	V	VI
1	.93	—.16	—.11	.14	.10	.84	.06	.08	—.08	—.14	—.12
2	.66	—.49	—.24	—.11	—.17	.65	—.22	.12	.12	—.18	—.08
3	.65	—.60	.15	—.22	—.16	.60	—.31	.24	.04	.15	.19
4	.93	.10	—.14	—.11	.13	.92	—.30	—.23	.14	.05	.05
5	.83	.32	.20	—.19	.03	.90	.27	—.08	—.16	.10	—.17
6	.88	.13	.11	—.34	—.03	.91	.21	—.12	—.11	—.03	.03
7	.92	.09	.04	.25	—.08	.92	.06	.13	.15	—.09	.05
8	.89	.23	—.08	.12	—.22	.93	.12	.08	—.12	.10	.15
9	.95	.04	.22	.22	—.03	.97	.17	.18	—.05	.11	.05
10	.94	.10	—.08	—.11	.13	.96	.17	—.06	.08	—.13	—.02
11	.94	.07	.22	.12	.03	.96	.09	—.07	.10	—.07	.05
12	.77	.33	—.40	.03	—.12	.83	—.20	.19	.04	.10	—.14
13	.93	.16	—.08	.06	.13	.84	.12	—.13	.28	.16	—.03
14	.66	—.21	.20	.14	.18	.77	—.15	—.28	—.21	—.11	.18

Table III lists the communalities h_j^2 and uniquenesses u_j^2 for the two castes. In both castes head width has the highest communality. This means that practically all of its variance is discernible in its correlations with other characters measured, and it shows almost no variance due to unique factors influencing the head width but none of the other characters of the study. The only high uniquenesses for the soldier caste are those for eye diameter and for the length of the second antennal segment. At least in the case of eye diameter this suggests one or more additional factors, acting on eye diameter but not on any of the other characters measured. This seems a reasonable consequence of the convergent reduction of the soldier eye in many different lines. There are five reasonably high uniquenesses of the imago caste, the largest two involving the second and third antennal segments. The data suggest that there are unique factors acting on each of these two characters.

The distributions of residuals from the factoring are noted in Table IV. It is found that the two distributions are very similar, even though five factors have been found for the soldiers and six for the imagoes. These residuals may be due to errors of estimate of the correlations, rounding errors in the factoring, and to very small common factors not influencing the variances of the characters enough to be detected in this study. The residuals are all small and their distributions are approximately normal.

Table V is the rotated factor matrix for the soldier caste. If ± 0.10 is taken as the null value for a loading, it can be said that factor A is determined by six characters on which it has no influence, B by nine characters, C by eight, D by nine, and E by nine. Thus all factors except A are rather well determined. Even A is determined better than the rule-of-thumb criterion suggested by Thompson (1939), namely, that the number of near-zero entries in each column should be as great as or greater than b, the number of factors in the study.

TABLE III—COMMUNALITIES AND UNIQUENESSES

	SOLDIER CASTE		IMAGO CASTE	
CHARACTER	COMMUNALITY h_j^2	UNIQUENESS u_j^2	COMMUNALITY h_j^2	UNIQUENESS u_j^2
1	.93	.07	.76	.24
2	.77	.23	.54	.46
3	.88	.12	.57	.43
4	.92	.08	1.00	.00
5	.86	.14	.95	.05
6	.92	.08	.90	.10
7	.92	.08	.90	.10
8	.91	.09	.93	.07
9	1.00	.00	1.00	.00
10	.93	.07	.98	.02
11	.95	.05	.95	.05
12	.87	.13	.80	.20
13	.92	.08	.84	.16
14	.58	.42	.78	.22

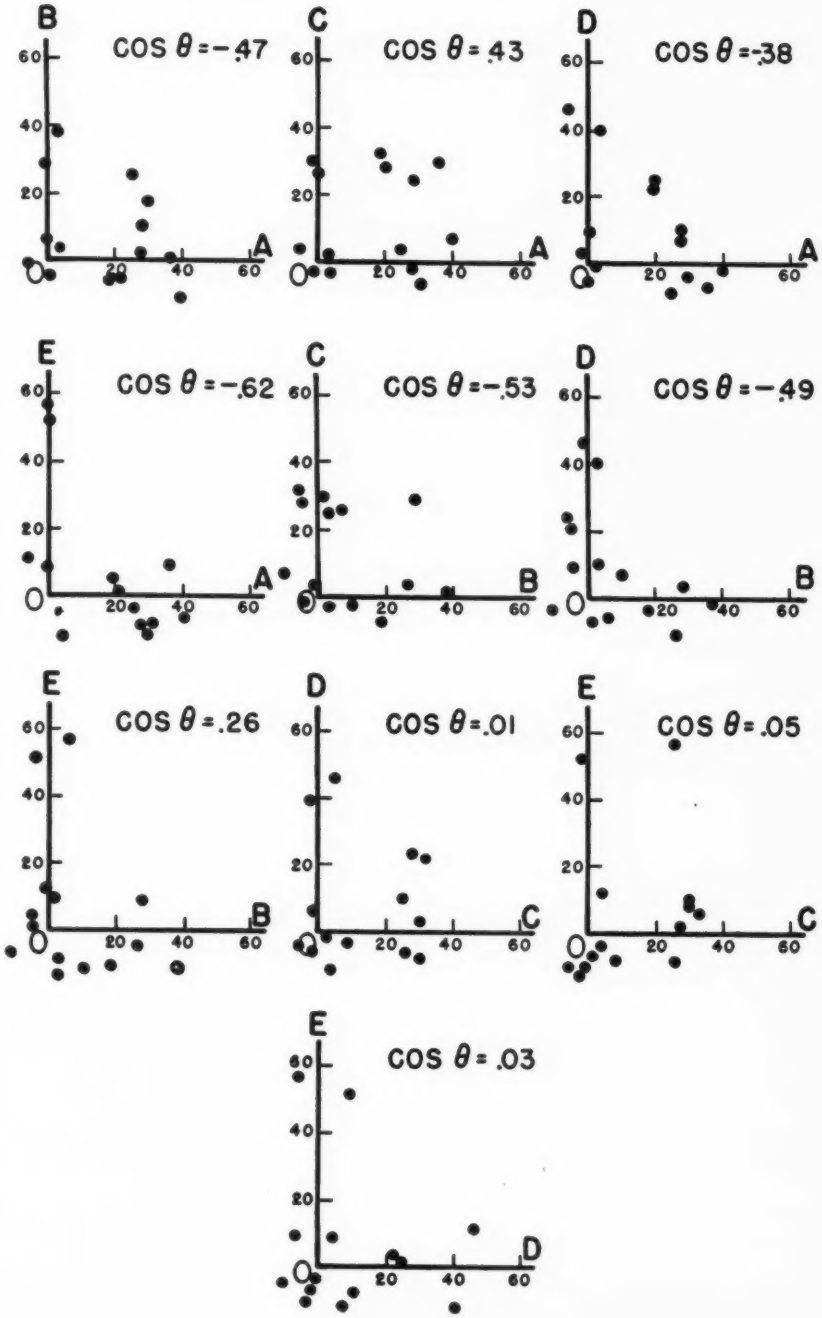
TABLE IV—DISTRIBUTIONS OF RESIDUALS FROM FACTORING

SIZE OF RESIDUAL	NO. OF SOLDIER RESIDUALS	NO. OF IMAGO RESIDUALS
.00	29	20
±.01	33	40
±.02	20	22
±.03	7	6
±.04	2	3

TABLE V—ROTATED FACTOR MATRIX V_{zj}

	SOLDIER CASTE				
	A	B	C	D	E
1	.36	.01	.30	.07	.10
2	.00	.06	.26	—.06	.57
3	.00	—.04	—.01	.09	.52
4	.19	—.05	.32	.22	.05
5	.04	.03	—.03	.40	—.12
6	—.06	—.01	.04	.46	.12
7	.25	.26	.04	—.11	—.04
8	.03	.38	.02	—.01	—.06
9	.30	.18	—.06	—.04	—.10
10	.20	—.05	.28	.24	.02
11	.28	.10	—.02	—.07	—.11
12	—.01	.28	.30	.04	.09
13	.28	.03	.25	.10	—.08
14	.40	—.11	.08	—.03	—.07

FIG. 3. Final positions, rotated soldier factors.


B
COS θ = −.47
C
COS θ = .43
D
COS θ = −.38
E
COS θ = −.62
C
COS θ = −.53
D
COS θ = −.49
E
COS θ = .26
D
COS θ = .01
E
COS θ = .05
E
COS θ = .03
0
20
40
60
A
B
C
D

Since the origin must lie in the subspace of $(b-1)$ dimensions which determines the factor, such a subspace can be found to fit exactly to any $(b-1)$ vectors. Hence the existence of such a subspace is suggested by numbers greater than or equal to b. In the soldier study b is five.

It should be noted that factors whose null set of characters B_p contain less than about $m-b$ elements are not discovered in a factorial analysis, where m is the number of measurements and b the number of factors. A primary factor for "general size," if it existed in the present study, would be of this sort, as there would be no characters whose variance it did not influence. If such a factor existed at the first-order level, then from a study based on b centroid axes, only $(b-1)$ linearly independent factors would be found by rotation. Since this was not the case in either of the present studies, it must be assumed that no such general size factor, having a relatively large degree of independence from the other primary factors, exists.

Table VI gives the rotated factor matrix for the imago caste. Here $b=6$, and the numbers of vectors defining each factor are: *A*, nine; *B*, nine; *C*, eleven; *D*, eleven; *E*, eleven; and *F*, nine.

Figures 3 and 4 show the "final positions" of the factor axes as seen in two-dimensional sections of the spaces. In the figures the angles θ_{pq} between each pair of factor axes are drawn as though they were right angles. The cosine of the actual angle c_{pq} between axes is noted with each section.

The matrices of rotation Λ relating each set of factor axes to its corresponding set of centroid axes are presented as Table VII.

The primary factors obtained by rotation are, typically, correlated with each other. The table of the correlations of these factors is given as Table VIII. Some of these correlations are remarkably high, but the linear independence of the factors

TABLE VI—ROTATED FACTOR MATRIX V_{im}

	IMAGO CASTE					
	A	B	C	D	E	F
1	.15	.21	.01	.16	—.11	—.02
2	.29	.28	.00	.05	—.01	—.05
3	.26	—.04	.05	—.04	.03	.37
4	.26	—.01	.32	.02	.31	—.01
5	.02	—.04	.05	.28	.04	.01
6	—.08	.06	.15	.06	.00	.05
7	.05	.25	—.07	—.06	.02	.11
8	—.02	—.02	.08	.01	—.04	.30
9	.02	.03	—.07	—.07	—.03	.28
10	—.03	.23	.04	.00	.05	—.03
11	.00	.17	.09	—.04	.10	.03
12	.39	.04	—.04	.23	.08	.11
13	.00	.00	—.02	.00	.37	.01
14	.06	.00	.49	—.02	—.02	.04

TABLE VII—MATRICES OF ROTATION

SOLDIER CASTE Λ_{sj}

	A	B	C	D	E
I	.20	.08	.16	.11	.09
II	—.17	.23	—.14	.29	—.56
III	.07	—.06	—.76	.21	—.38
IV	.58	.40	—.07	—.90	—.42
V	.77	—.88	.61	.21	—.60

IMAGO CASTE Λ_{im}

	A	B	C	D	E	F
I	.13	.09	.10	.08	.06	.09
II	—.75	.09	—.40	—.13	—.11	.01
III	.22	.27	—.72	.01	—.50	.51
IV	—.09	.33	—.45	—.42	.64	—.20
V	.11	—.90	—.08	.29	.55	.48
VI	—.60	—.03	.32	—.85	—.13	.68

TABLE VIII—CORRELATIONS OF PRIMARY FACTORS

SOLDIER CASTE

	A	B	C	D	E
A	——				
B	.72	——			
C	—.27	.24	——		
D	.82	.84	.00	——	
E	.75	.34	—.40	.50	——

IMAGO CASTE

	A	B	C	D	E	F
A	——					
B	—.62	——				
C	—.50	.77	——			
D	—.80	.88	.71	——		
E	—.56	.86	.66	.78	——	
F	—.57	.90	.72	.85	.82	——

FIG. 4. Final positions, rotated imago factors.

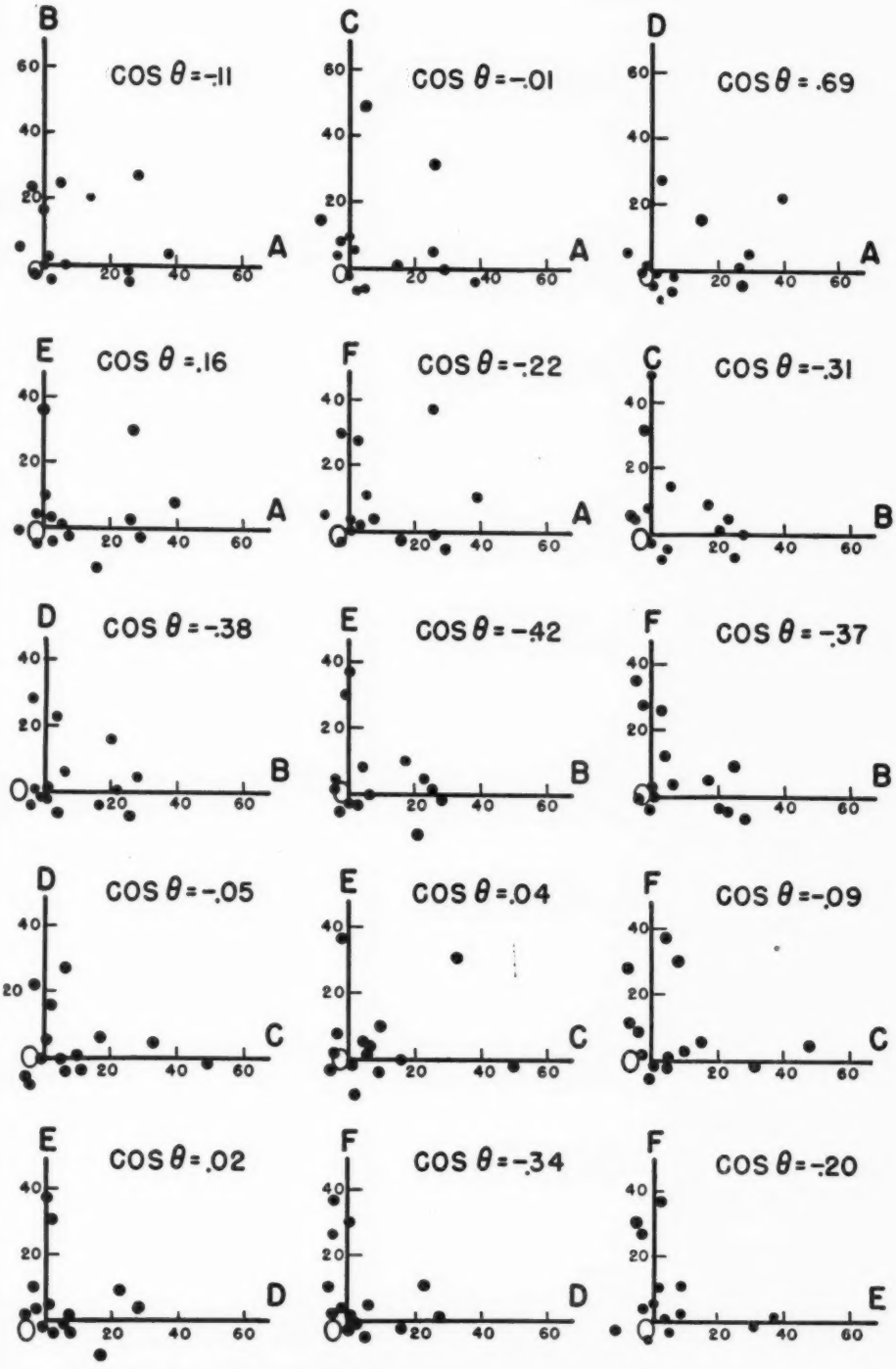

B
COS θ = -.11
A
C
COS θ = -.01
A
D
COS θ = .69
A
E
COS θ = .16
A
F
COS θ = -.22
A
C
COS θ = -.31
B
D
COS θ = -.38
B
E
COS θ = -.42
B
F
COS θ = -.37
B
D
COS θ = -.05
C
E
COS θ = .04
C
F
COS θ = -.09
C
E
COS θ = .02
D
F
COS θ = -.34
D
F
COS θ = -.20
E
0
20
40
60

TABLE IX—SECOND ORDER DOMAIN

	SOLDIER CASTE	
	I	II
A	.96	.02
B	.71	.64
C	—.23	.58
D	.85	.41
E	.78	—.39

	IMAGO CASTE	
	I	II
A	—.72	.38
B	.96	.19
C	.77	.13
D	.95	—.25
E	.86	.17
F	.91	.21

seems clear enough. No serious change need be made if two of the factors should eventually be regarded as only one, but there would then be the possibility of a linearly independent general factor at the primary level, which does not seem, at present, to be the case in either study. These correlations were then factored by the centroid method to obtain the second-order centroid matrix for each caste. The results are shown in Table IX. When these loadings for the soldier caste are plotted against each other (Fig. 5), using one centroid axis as the abscissa and the other as the ordinate, no grouping of the primary soldier factors is evident. A comparable plot (Fig. 6) for the imago factors, however, indicates a group consisting of factors *B*, *C*, *E*, and *F*, which could

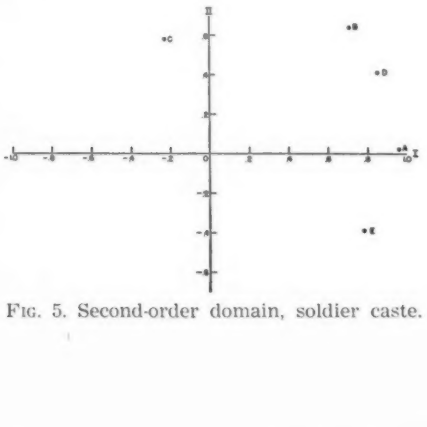


FIG. 5. Second-order domain, soldier caste.

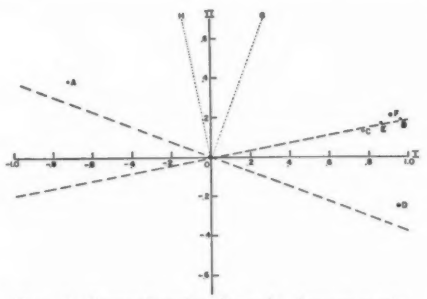


FIG. 6. Second-order domain, imago caste.

be assumed to lie in one subspace including the origin (in this two-dimensional example the subspace is a line). These second-order factors are used to account for the correlations among the primary factors.

The lack of structure corresponding to a group factor in the soldier study could be interpreted as indicating one or more general factors there. In the imago study what seem indicated are a bipolar second-order group factor relating the first-order factors *A* and *D*, and a general factor.

All second-order results in studies this small must be regarded as tentative and suggestive only. The addition of a few more characters might increase the number of first-order factors and alter the conclusions regarding the second-order domains.

Table X lists the evaluations of the *Proglyptotermes* individuals of the soldier

TABLE X—ALPHA PROJECTIONS OF *PROGLYPTOTERMES* SOLDIERS

K. atratus	.79
K. banksiae	1.22
K. brouni	.99
K. castaneiceps	1.12
K. gracilidens	.73
K. hilli	.98
K. longiceps	.87
K. longus	1.41
K. pallidinotum	1.52
K. rufinotum	1.00
K. sordwanae	1.32
K. spoliator	1.22
K. tillyardi	1.19
K. umtate	1.15
K. n. sp. (Ihosy)	1.06

caste for the axis α discussed in the succeeding section of this paper.

Discussion and Conclusions

Factor-analytical methods can probably make a substantial contribution to the solution of problems of character evaluation. One advantage of their application is that of parsimony. A relatively large number of observed characters can be reduced, practically speaking, to a considerably smaller number of parameters. In the present study the original fourteen measurements were reduced, largely, to five parameters for the soldier caste and to six for the imagoes. Much of the error variance is eliminated along with unique factors affecting only one measurement. The use of centroid evaluations permits the individuals to be located as points in a space whose axes are orthogonal to each other and which represent statistically independent parameters. A much more significant addition to biological knowledge is gained, however, by an examination of the rotated factors. These can, in some cases, be subjected to interpretations as causative agencies or as trends accounting for the correlations of the characters.

It does not seem feasible in the present paper to discuss in great detail the results obtained. Instead the results will be very briefly summarized and sampled here. In the present study the soldier factors are more easily interpreted, on the whole, than are the imago factors. This is probably due to the well-known fact, true rather generally throughout the order Isoptera, that the soldier undergoes a variety of obviously adaptive changes, whereas the imago caste is more conservative.

Of the five factors discovered for the soldier caste, three are distinctly regional in nature: factor *B*, a head-volume factor; *D*, a leg factor; factor *E*, an antennal factor. The other soldier factors, *A* and *C*, are not limited in their influence to a regional group of characters, but operate on a variety of characters distributed over the body. Of six imago factors, only one, factor *F*, shows strong regionality in its operation. The other five operate on measurements on various parts of the body.

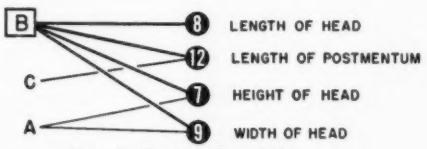


FIG. 7. Factor *B*, soldier caste.

The five soldier factors are all interpretable in terms of adaptive trends for the genus as a whole. Of the six imago factors only two seem probable as representing adaptive trends in the imago. The other four factors, and to some extent these two as well, are related in a very interesting way to the factors discovered for the soldier caste.

Factor *B* of the soldier caste affects the four measurements shown in Figure 7: the three dimensions of the head and the length of the postmentum, which runs along and constitutes a part of the floor of the head capsule. Thus it is a factor with a distinctly regional influence, affecting all dimensions of the head. Apparently, the width of the postmentum is independent of this factor. The existence of factor *B* may be interpreted in any of three ways which are not necessarily mutually exclusive: (1) it may be that a certain proportionality among the head measurements tends to be maintained in spite of any other changes in the body; (2) there may be a directional tendency toward increase in head volume for some or all the species; or (3) there may be a tendency for head-volume decrease for some or all the species. Another possibility is that some early dichotomy of the genus, through selective or random acquisition of different alleles in the two lines, resulted in two rather discrete groups of species whose principal difference is head volume. If this were the case one would expect a marked bimodality in the distribution of the individual evaluations for factor *B*. Since no such bimodality is evident this

fourth possibility can be eliminated. It is not possible, as a result of the present study, or on the basis of other facts known about the genus, to distinguish clearly among the first three possibilities; but the third, head-volume reduction, seems most likely.

Factor *A* for the soldier study is an interesting example of a non-regional factor. It affects eight of the fourteen characters studied. The eye in the soldier caste is undergoing evolutionary regression, while in the imago caste, with the same genetics, the compound eyes are maintained as functional structures. The eye shows considerable unique variance, as suggested by the factor *U* in Figure 8, but 58 per cent of its variance is due to common factors included in this study. These findings strongly indicate that much of the regressive decrease in eye diameter in the soldier caste is attributable to the selection of alleles which happen to be deleterious to the soldier eye but which have pleiotropic effects of selective advantage in reducing the cross-sectional area of the soldier. The entire combination of characters involved in factor *A* amounts to a decrease in this cross-sectional area, fitting the soldier caste to more efficient function in small burrows of subcircular section.

Turning to imago factors, it is found that these are more difficult to interpret as functional adaptations of the imago caste, but that a number of them are closely related to the soldier factors. The closest such relationship is that between

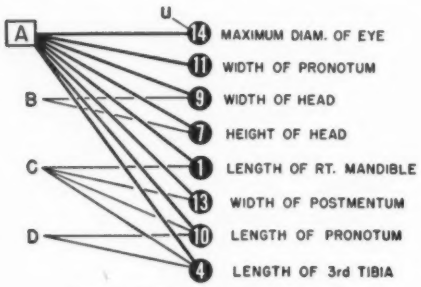


FIG. 8. Factor *A*, soldier caste.

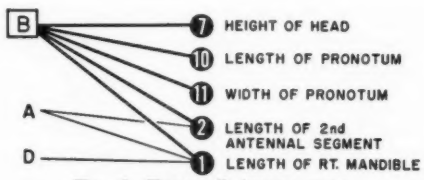


FIG. 9. Factor *B*, imago caste.

imago factor *B* and soldier factor *A*. The coefficient of correlation $r = .74 \pm .08$ for the 37 species in which both soldier and imago specimens were measured. Imago factor *B* (Fig. 9) affects four characters homologous to those affected by soldier factor *A*. It also affects the length of the second antennal segment, regionally almost contiguous with the head. The imago eye, head width, postmentum width, and tibia length are independent of imago factor *B* although their homologues are affected by soldier factor *A*.

The interpretation is that an obviously adaptive trend in the soldier caste is reflected by a trend in the imago caste affecting some but not all the homologous characters, and bringing in one additional character. Imago factor *B* may have some adaptive value in the imago caste but the relation is not clear. In this case, the alleles that have been selected seem to be those whose action is similar in sense in both castes, thus especially those alleles whose major contribution (other than eye reduction) to development is made prior to the time of soldier differentiation. In the case of a different relationship between factors of soldier and imago caste, the correlation is negative, suggesting the selection, primarily, of alleles acting in soldier differentiation.

This sample of the factors of the present study should suffice to indicate the extremely interesting possibilities which factor analysis offers for the interpretation and evaluation of characters.

A different application of multiple factor analysis lies in the identification of categories of organisms. A rotational search for groupings of species in the space described by the centroid evalua-

tions was made. Since this is the first time such a technique has been applied in factor analysis, conclusions based on the findings must be viewed with some reserve. For this and other reasons, only the largest, most obvious streaks were examined.

In the soldier study an axis α was found on which a group of fifteen species had sub-equal projections. The difference between the mean for this species-group and for the rest of the genus is highly significant. This group of fifteen species, along with several others not in the soldier study, had previously been assigned to the genus *Proglyptotermes* by Emerson (Kirby, 1949) on the basis of a survey of the imago caste. Its members are, in general, smaller and darker than *Kalotermes* and always have an aroleum (some *Kalotermes* lack this structure). Although it had appeared in the literature its status was still uncertain. Kirby found corroborative evidence in the similarity of their intestinal flagellates. This study confirms, for the soldier caste, the existence of such a category as *Proglyptotermes*, but further study is needed before a final decision can be reached as to whether it should be designated as a genus or as a category of subgeneric rank within *Kalotermes*.

A comparable rotational search of the imago evaluations suggested the existence of the same group, but it is not so clearly defined here as in the soldiers. Apparently, additional, more critical characters must be used to find reliable criteria for distinguishing *Proglyptotermes* imagoes.

It should be stated that multiple factor analysis permits the identification of character correlations with factors or trends which can be considered the causative agents accounting for the correlations. It presupposes the additive combination of linearly related causes. Biological factors can hardly be supposed to have exactly these properties; but this must be approximately so, or interpretable results such as those reported here could not be found.

It is hoped that the method of factor analysis can supplement the more usual systematic techniques and permit a better description of some of the millions of evolutionary experiments in which nature has engaged.

Summary

By means of multiple factor analysis and related techniques the genus *Kalotermes* was examined in an attempt to elucidate its systematic structure. Factor analysis can be of great aid in evaluating characters. By its use five primary factors have been found for the soldier caste and six for the imago caste of *Kalotermes*. Interpretations of a sample of these are presented, showing their relation to evolutionary trends in the genus and to regressive evolution and pleiotropism.

The method of multiple factor analysis is discussed briefly as it has been applied to systematic problems. A brief set-theoretical account of Thurstone's simple-structure concept is developed. An extension of the methods of multiple factor analysis is employed in which a rotational search is made for groupings among individual evaluation points in the common-factor evaluation space. The existence of a previously suspected genus or subgenus, *Proglyptotermes*, is demonstrated in the soldier caste.

REFERENCES

AHMAD, M. 1950. The phylogeny of termite genera based on imago-worker mandibles. *Bull. Am. Mus. Nat. Hist., 95,* 37–86.

BURT, C. 1938. The analysis of temperament. IV. Physical signs of temperament. *Brit. J. Med. Psychology, 17,* 184–187.

——— 1941. The factors of mind. Macmillan Co., New York.

COHEN, J. 1938. Determinants of physique. *J. Mental Sci., 84,* 496–512.

——— 1939–1941. Physique, size, and proportions. *Brit. J. Med. Psychology, 18,* 323–327.

HAMMOND, W. H. 1942. An application of Burt's multiple general factor analysis to the delineation of physical types. *Man, 42,* 4–11.

HOLZINGER, K. J., and HARMAN, H. H. 1941. Factor analysis. Univ. of Chicago Press.

KELLEY, T. L. 1935. Essential traits of mental life. Harvard Univ. Press, Cambridge, Mass.

KIRBY, H. 1949. Devescovinid flagellates of termites. V. The genus *Hyperdevescovina*, the genus *Bullanympha*, and undescribed or unrecorded species. *Univ. Cal. Publ. Zool., 45,* 319–422.

MCCLOY, C. H. 1940. An analysis for multiple factors of physical growth of different age levels. *Child Development, 11,* 249–277.

MOORE, T. V., and HSU, E. H. 1946. Factorial analyses of anthropological measurements in psychotic patients. *Human Biology, 18,* 133–157.

REES, W. L., and EYSENCK, H. J. 1945. A factorial study of some morphological and psychological aspects of constitution. *J. Mental Sci., 91,* 8–21.

THOMSON, G. H. 1939. The factorial analysis of human ability. Houghton Mifflin, New York.

THURSTONE, L. L. 1931. Multiple factor analysis. *Psychological Review, 38,* 406–427.

——— 1945*a*. Multiple factor analysis. Univ. of Chicago Press.

——— 1945*b*. Factor analysis and body types. *The Psychometric Lab.*, No. 24, 1–7.

——— 1946. Analysis of body measurements. *The Psychometric Lab.*, No. 29, 1–13.

TUCKER, L. 1938. *Psychometrika, 3,* 189–197.

WRIGHT, S. 1918. On the nature of size factors. *Genetics, 3,* 367–374.

——— 1921. Correlation and causation. *J. Agricultural Res., 20,* 557–585.

——— 1923. The theory of path coefficients—a reply to Nile's criticism. *Genetics, 8,* 239–255.

——— 1932. General, group, and special size factors. *Genetics, 17,* 603–619.

——— 1934. The method of path coefficients. *Annals Math. Statistics.* Charles Griffin, London.

Although the mathematical nature of this paper makes it slow reading, the technique of multiple factor analysis promises to be of wide utility in systematics for reducing complex sets of data to a relatively small number of causative factors. At the time of his death on October 8, 1952, **CLYDE P. STROUD** was Associate Biologist in the Biological and Medical Division of the Argonne National Laboratories, Chicago. This paper is a portion of the dissertation accepted for the degree of Doctor of Philosophy by the Department of Zoology, University of Chicago. Financial support for portions of the investigation was given by the Dr. Wallace C. and Clara A. Abbott Memorial Fund of the University of Chicago. The dissertation was written under the direction of Dr. Alfred E. Emerson who also edited the manuscript after the death of Dr. Stroud. Advice concerning the mathematical techniques was given by Dr. Louis L. Thurstone and Dr. Sewall Wright. This paper was presented at the symposium on "Statistical Problems in Animal Experimentation," December 27, 1951.

An Improved Graphical Analysis

(*Concluded from p. 56*)

HUBBS, CLARK. 1952. A contribution to the classification of the blennioid fishes of the family Clinidae, with a partial synopsis of the Eastern Pacific forms. *Stanford Ichth. Bull., 4,* 41–165.

——— 1953. Revision and systematic position of the blenniid fishes of the genus *Neoclinus*. *Copeia,* 1953, 11–23.

OLIVER, J. A. 1948. The relationships and zoogeography of the genus *Thalerophis* Oliver. *Bull. Am. Mus. Nat. Hist., 92,* 157–280.

PITELKA, F. A. 1950. Geographic variation and the species problem in the shore-bird genus *Limnodromus*. *Univ. Calif. Publ. Zool., 50,* 1–108.

RUTHVEN, A. G. 1908. Variation and genetic relationships of the garter-snakes. *U. S. Nat. Mus. Bull.* 61.

SIMPSON, G. G., and ROE, ANNE. 1939. Quantitative zoology. McGraw-Hill Book Co., New York and London.

STORER, R. W. 1952. A comparison of variation, behavior and evolution in the sea bird genera *Uria* and *Cepphus*. *Univ. Calif. Publ. Zool., 52,* 121–222.

TORDOFF, H. B. 1952. Notes on plumages, molts, and age variation of the red crossbill. *Condor, 54,* 200–203.

CARL L. HUBBS is Professor of Biology at the Scripps Institution of Oceanography, University of California, La Jolla. **CLARK HUBBS** is Instructor in the Department of Zoology, University of Texas, Austin. In the preparation of this paper advice and encouragement were received from statisticians Cecil C. Craig and George F. Lunger, and from several biologists, including Lee R. Dice. Contribution from the Scripps Institution of Oceanography, New Series, No. 635.

"Methods and Principles . . ."

CARL L. HUBBS

METHODS AND PRINCIPLES OF SYSTEMATIC ZOOLOGY. By Ernst Mayr, E. Gorton Linsley, and Robert L. Usinger. McGraw-Hill Publications in Zoological Sciences. McGraw-Hill Book Co., New York, Toronto, London, 1953. ix + 328 pp., 45 figs. $6.00.

TIME has been ripe for the preparation of a general treatise on systematic zoology. The field of general systematics has at long last been taking shape. The young Society of Systematic Zoology has grown vigorously and is filling a very obvious need in stimulating and correlating thought. One of the first projects of the Society was the sponsorship of a book that would expound the principles of the general field. There need be no great regret over the circumstance that the Society has been anticipated in this regard; there is room for several such treatises. It is understood that the University of California entomologists Linsley and Usinger had a book well under way when they heard that the American Museum ornithologist Mayr was also preparing one. The three, all interested in general systematics as well as in their specialties, then joined hands to produce a work that the Society of Systematic Zoology might well endorse.

This book has the freshness and vigor, and some of the defects, of a pioneering work. It treats broadly, but in some respects not comprehensively or evenly: (1) history, concepts, and categories, (2) procedures, and (3) nomenclature. It stresses the art of taxonomy—the classifying and naming of animals—and largely elides the fundamental principles of speciation and phylogeny, which many of us would include in the broader circle of systematics, but which the authors, drawing the overlapping circles differently, would probably relegate largely to the field of evolution. They define and treat "taxonomy" as the interchangeable equivalent of "systematics."

In accordance with their taxonomic philosophy, some readers will be disappointed with the omission or curtailed treatment of various subjects or points of view that are dear to them. There is no sound weighing of the relative merits and defects of splitting and of lumping, merely a repeated indication of a strong bias toward lumping. Ecological speciation is largely denied or avoided, as in previous works by the senior author. Experimental methods are accorded little space or emphasis, comparative serology is only briefly treated, and other biochemical methods are barely mentioned. There is little indication that group revisions, particularly for less completely classified animals, are apt to be more significant than faunal studies; and there is no adequate emphasis on the sound principle that it is desirable to study a species or group thoroughly throughout its range. The extraordinarily high taxonomic value of genitalial characters and the low trustworthiness of nutritional adaptations are not clearly brought out. The use of calculating machines, standard in some fields, is not mentioned. Little attention is paid to the analysis of regression or to other refined methods of studying variations. Sharp distinction is not drawn between the measurement of degree of difference (by standard deviation) and significance of difference (by standard error). The erroneous idea that meristic counts are fully discrete (strictly noncontinuous) is not denied. Descriptions and especially keys are indicated as designed solely or almost wholly for the identification of specimens, whereas they may be valuable also for the portrayal of relation-

ships and for the reporting of data of value for speciational and phylogenetic analyses. Photographic illustrations are definitely underrated. Although it is emphasized that names for familial and higher categories are plural, the more needed advice is not stressed that generic names, despite very frequent misuse, are always singular. Missing are references to several important treatises, including Schenk and McMasters' book *Procedure in Taxonomy* as well as the two scholarly papers by Walther Miller and by Frederic E. Clements, on the classical basis for the formation of scientific names. It would have been useful to indicate that systematists should obtain large numbers of reprints and should distribute them widely, and to state that reprint collections are particularly useful in systematic research. No attention is given to systematic methods that are distinctive of the study of certain groups, such as Protozoa and parasitic worms.

As would be expected, the authors have drawn almost exclusively on ornithology and entomology for examples. In general this is not a serious defect, for such examples are usually adequate to illustrate the procedure or principle involved. Many a systematist, however, will feel that his field has been slighted, particularly in the history of zoological taxonomy and in the treatment of subjects in which he will think that pioneering and outstanding work has been done in his own field. He may think that some of the many examples drawn from ornithology are less effective than they would have been had they been taken from his field, in which he believes that greater progress has been made, for example in the statistical study of races and in the analysis of natural interspecific hybridization. He will recall that his studies are based on goodly series of whole specimens, rather than on individual study skins, and that for this and other reasons, a large array of characters has been utilized in speciational and phylogenetic analyses. Such a systematist may feel a bit annoyed on being reminded so frequently of the completeness and pre-eminence of bird systematics.

Most of the defects in the book are relatively minor, however, and are subject to correction in a new edition. They are more than balanced by the adequate coverage of most taxonomic questions, by the many wise statements, and by much sound advice. The writing is crisp and clear, the definitions precise, and the examples numerous. Real systematic understanding is shown, particularly in the sharp distinction of true taxonomic units from variations that have not formed populations. Extremely helpful are the descriptions of various methods (1) for plotting forms and variations geographically and phylogenetically, (2) for the statistical and graphical analysis of variation (too brief), and (3) for presenting keys and phylogenies in pictorial, graphical, and text form. The directions for preparing taxonomic papers should prove valuable, especially for beginners, but should have stressed the desirability of following the format approved by the journal in which they will be published. The thorough and temperate discussion of zoological nomenclature is very timely. The final chapter on ethics in taxonomy should be read, digested, and followed by old-timers as well as novices.

People and Projects

Dr. Ernst Mayr, Curator of the Whitney Rothschild Collection, American Museum of Natural History, has been appointed Alexander Agassiz Professor of Zoology in the Museum of Comparative Zoology, Harvard University. Mr. James C. Greenway, Jr., has been appointed Curator of Birds, succeeding the late James L. Peters, and Mr. Raymond A. Paynter, Jr., has been appointed Assistant Curator of Birds.

The University of Michigan's Museum of Zoology will give its entire crustacean collection to the U. S. National Museum, according to a recent announcement by President Harlan Hatcher. The collection is a rather large one with particularly good specimens from the regions of the Great Lakes and the Ozark Plateau. Since 1933, however, the collection has been largely inactive, the Regents were told by J. Speed Rogers, director of the Museum of Zoology, and is no longer adequate to form the basis for important research work. In view of this, it is felt that the collection will be more useful both to the public and to research biologists when made available through the U. S. National Museum, which has long been a major center for work on the Crustacea. The Museum of Zoology now will concentrate its energies and resources on mammals, birds, reptiles and amphibians, fish, insects, and mollusks, in each group of which it has notable collections.

On January 1, 1953, the two national entomological societies, the former Entomological Society of America and the American Association of Economic Entomologists, were united. The resultant single society, representing all phases of the science of entomology, has taken the appropriate name, the Entomological Society of America. Each of the amalgamating societies brings a distinguished reputation into the new organization. With entomologists of the state agricultural experiment stations taking the initiative, the American Association of Economic Entomologists was organized at a meeting in Toronto, Canada, in 1889. The Entomological Society of America was organized in 1906 in response to a need for a society in which emphasis would be placed on noneconomic phases of entomology. Professor J. H. Comstock, of Cornell University, himself a charter member of the Association, was chosen as the first president of the Entomological Society; and the two societies have held what were to all intents and purposes joint meetings every year, with the exception of 1942 and 1945.

Although the two organizations had supposedly different interests, in reality these interests overlapped widely; and as time passed it became increasingly evident that no clear line of demarcation between the two fields could be recognized. Merger of the two societies was considered many years earlier, but it was not until 1949 that a serious effort in that direction was undertaken. That year each society appointed a committee of three men to consider the feasibility of such a merger and to make recommendations to their respective societies. After presenting preliminary reports in favor of amalgamation at the Tampa, Florida, meetings in December 1949, the two committees were continued as a joint committee to draw up a proposed Constitution and By-Laws, which were presented to the membership of each society at Denver, Colorado, in December 1950, together with recommendations for procedure to effect the amalgamation. After due deliberation the

merger proposal was submitted, by mail, to the membership of each society early in 1951. The Association, in 1951, and the Society, in 1952, voted to ratify the new Constitution, making it possible for the newly constituted Entomological Society of America to begin functioning as of January 1, 1953.

During the current year an Interim Governing Board, composed of the executive committees of the two former organizations, is conducting the affairs of the Society, and a full-time executive secretary will be selected by the Board. Dr. Charles E. Palm, of Cornell University, is president of the Society for 1953, and Herbert H. Ross, of Illinois State Natural History Survey, is president-elect.

The Society will continue to publish the *Annals of the Entomological Society of America* and the *Journal of Economic Entomology*. Each of these journals will appear in its forty-sixth volume in 1953. The *Index of American Economic Entomology* and *Memoirs of the Thomas Say Foundations* will continue to be published intermittently. *Entoma*, a directory of insect and plant disease control, will be continued, and a new monthly *Bulletin*, to contain current items of general interest, will also be issued.

Erratum. H. B. Hungerford, president of the Society of Systematic Zoology, was erroneously stated (SYSTEMATIC ZOOLOGY, *2*, 46) to be head of the Department of Entomology at the University of Kansas. Prof. Hungerford was head of the department for 25 years, but recently resigned from that office in order to devote more time to research.

The project "Insects of Micronesia" (SYSTEMATIC ZOOLOGY, *1*, 182), under the direction of J. Linsley Gressitt, has been transferred from the Pacific Science Board to the Bernice P. Bishop Museum, Honolulu, where Dr. Gressitt holds the position of entomologist. The museum has been awarded a grant of $15,200 by the National Science Foundation to help support the project for the next 18 months. The field work is being completed with the balance of funds from the Board's contract with the Office of Naval Research, with N. L. H. Krauss, Dr. Gressitt, and J. F. Gates Clarke each spending a few months in the Caroline Islands during 1952-53. About 400,000 specimens have been assembled from Micronesia. Over 100 specialists, representing about 50 institutions in a dozen countries, are now associated with the project. The reports will be published as a special series of the Bishop Museum, with each author's work as a separate issue.

SYSTEMATIC ZOOLOGY is published quarterly by the Society of Systematic Zoology. Its purpose is threefold: To publish, and therefore to encourage the preparation of, contributions on basic aspects of all fields of systematics, principles and problems; to provide a suitable forum for discussion of the problems of the systematist and his methods; and to report as news the other activities of the Society of Systematic Zoology.

Contributions of the following types are solicited: Papers on principles and the applications of principles of wide implication and general interest in any phase of systematics, such as comparative anatomy, zoogeography, paleontology, taxonomy, classification, evolution, or genetics; discussions of methods, specific problems, and activities of systematists; discussions of new books and monographs; and news of systematists, organizations interested in systematics, research and teaching programs, expeditions, collections, meetings, and anything else of interest to systematists.

Major articles should be from 1500 to 10,000 words in length. Discussion articles should not be over 400 words unless of very general interest. Contributors are encouraged to submit line drawings and diagrams to illustrate their articles. Half-tones may be accepted where necessary to the article.

THE PUBLICATION FUND

A Publication Fund was established to help in the initiation of this journal. It consists entirely of donations from the members. It is hoped that it will be a permanent fund for use in other publication programs as well. For this reason further contributions of any amount will be welcomed. At present this fund is restricted to use for SYSTEMATIC ZOOLOGY, under the supervision of the Council.